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THE GENE

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WITHOUT running the risk of exaggerating the geneticists may claim to have finally settled the following facts about the gene: 1. its real existence as a rather stable unit; 2. its position within the chromosomes of the cell; 3. the orderly arrangement of the genes within each chromosome; 4. the transmission of the genes through the generations of cells and individuals, generally without change of the nature of the gene; 5. the connection of definite genes as cause with every conceivable type of morphological and physiological character in the organism as effect. Thus the conception of the gene has become as firm a basis for the study of heredity as the conception of the atom for the study of physics. The next problems which have to be solved concern the nature of the gene and its action in producing the hereditary characters. The study of these problems has only begun. There is at present no way visible for a direct attack upon the gene which could reveal its nature. Only indirect ways are available, which might lead to more or less definite conclusions. Already quite a number of facts have been accumulated, which might serve as a starting point for further investigation. The following review will examine such facts and try to correlate them. The present writer has consistently worked in this direction and developed definite conclusions from experimental evidence, which so far as he can see are still the only ones covering the whole body of problems. He may therefore be excused if his own interpretations are placed in the foreground. However, the facts which will be recorded are facts, and everybody is welcome to give them another interpretation, provided it covers the same ground and is a better one.

A number of different ways are visible for the attack on our problem. In our opinion by far the best ought to be the study of the effects of the same gene in different quantities. If a gene has a different effect when present in different quantities and if these effects can be shown to follow any law a very considerable step will have been made towards the understanding of the action of the gene. This way of analysis was first opened by

the present writer; we may, therefore, begin with an evaluation of his primary facts and conclusions, which will be followed by a critical review of the different types of further evidence on the same point. These sections (A, B) will be followed by a review of the other methods of attack upon our problem and their results as we see them (C-F). Two short general sections (G, H) will conclude the paper.

A. THE EFFECTS OF THE SAME GENE IN DIFFERENT QUANTITIES

I. The genes of sexual differentiation

In a series of papers from 1911 to 1927 the present writer analyzed the case of experimental intersexuality in the gipsy-moth, which furnished him the first notions about the action of a gene. Neither the experiments nor the conclusions will be reviewed here in detail (A rather complete review up to 1926 is found in Goldschmidt, '27); only that part will be mentioned which is decisive for the present problem: viz. the proofs for our claim that in these experiments really different quantities of a gene were studied and further that these different quantities were linked up with typical effects.

One of the fundamental results of this work was the experimental proof that in dioecious animals both sexes contain the determiners or genes for the production of either sex and that the actual sex is determined by a quantitative relation or balance between these two sets of genes. As one of them (M in the Abraxas type, F in the Drosophila type) was shown to be situated in the X-chromosome and therefore present in one or two quantities, the other (F in the Abraxas type and M in the Drosophila type) being outside of the X-chromosome and always present in the same quantity, it became clear that the mechanism of the sex-chromosomes furnishes a method of associating the same dose of the one sexual determiner with either one or two doses of the other. As the two doses of the determiner within the sex chromosomes produce the sex of their own type (male—*Abraxas*, female—*Drosophila*), but with one dose present sex follows the determiners outside of the sex-chromosomes, the sexual decision is brought about by the relative quantities of the two types of genes according to the formula $F \gtrless {M \atop MM}$ (*Abraxas*) and $M \gtrless {F \atop FF}$ (*Drosophila*). This conclusion, which was inevitable from the writer's experiments, has since been corroborated by all the new evidence. Here then was the possibility of studying the effects of one gene in different quantities, other things remaining equal. We speak here of one gene F or M. Leaving aside certain autosomal modifiers which we found (and which were later similarly found by Bridges in *Drosophila*), we cannot prove experimentally that F and M are single genes. But all our large experimental evidence shows that they are inherited like single genes. For our conclusions it is then irrelevant whether the symbols F and M are the equivalents of single genes or of an unknown group of inseparable genes. If it is proven that the formulae in question are the true representation of the case—and this is proven—it follows that the quantity of each of these genes plays an important rôle in the action of the gene: a quantitative relation or balance has no meaning except in connection with the absolute quantities back of the proportion.

The full proof for these conclusions was derived from the experiments, in which forms were crossed which are distin-

guished by different but typical quantities of the F and M genes. The results are different combinations in which the normal balance as expressed in the above given formulae is disturbed because the quantity of M or F which has been introduced into the cross no longer balances the quantity of the other set (F or M). The result is male or female intersexuality of a definite degree up to sex-reversal in both directions, everything occurring in a most orderly way and completely in the hands of the experimenter. The decisive point is then, whether in these experiments a real proof has been furnished that the results are produced by the presence of different and typical quantities of the F and M genes.

There is indeed a very large amount of experimental evidence which consistently leads to the same conclusion. We may mention the fact that such diversified but typical results of a given cross as will be enumerated presently are completely explained and expected members of a series, namely: only males; only females; males normal and females of a definite degree of intersexuality; females and males *vice versa;* half the females normal, half intersexual; half or another ratio of males intersexual; 3 males: 1 female; 3 females: 1 male; the same 2: 1; only females and a few intersexual males etc. Further, if a given race is crossed in one direction with another test-race we can predict every result of crosses with all other races in every direction. Only this type of circumstantial evidence may be mentioned. But there are also direct proofs of the following types. First: The relative quantities of F and M for different races were determined from experiments on female intersexuality and the races arranged according to the values found. From the very different experiments on male intersexuality a similar determination was made; the two were always found to coincide. Further: Individuals of male gametic constitution (F) MM may be built up in which F comes from a race with high quantities of this gene and both M's from a race with a very small quantity of M. The result is a female in spite of male gametic constitution. We may then build up individuals in which F and one M remain as before but the other M is furnished by a third race of known behavior. The result, namely the production of male intersexes of a definite degree or normal males according to the race which furnishes the M, puts out of question any other explanation; it can only be understood, if really definite and typical quantities of F and M are involved. As a matter of fact any other interpretation of our experiments has never been proposed. Moreover it has become still more certain since triploid intersexes have been produced (Standfuss, '14; Bridges, '22; Goldschmidt and Pariser, '23; Meisenheimer, '24; Seiler, '27) where the different gene quantities are visibly given in the chromosome sets. (Full discussion in Goldschmidt, '27.) Thus it is claimed as a fact that in our work on intersexuality different quantities of one gene have been studied.

Now for the effect of these different quantities of genes. It has been demonstrated that intersexuality results if development of the individual proceeds up to a certain point, the turning point, with one sex and is finished after the turning point with the other sex, a demonstration which already has been produced for the intersexes of *Bonellia* by Baltzer ('14). The degree of intersexuality up to complete sex-reversal is determined by the earlier or later position of this turning point. This is not a hypothesis but a fact proved by morphological and embryological study (see

Goldschmidt, '17, '20c, '22, '23c, '27b). Thus we have the four sets of facts: 1. At the beginning of development two sets of genes, male and female, are present in definite quantities; 2. The relation or grade of balance of these two quantities decides whether normal sex is developed or a definite step in a continuous series of intersexuality up to sex-reversal; 3. Normal sex, increasing intersexuality and sex-reversal are determined by the non-occurrence or earlier and earlier incidence of the turning point; 4. The time of incidence of the turning point is a simple function of the relative quantities of the *M* and *F* genes, namely of the degree of their unbalance. These facts, based on an extraordinarily diversified but always consistent set of experimental and morphological data, are linked together by the conclusion that *a*) both the *F* and *M* genes produce chains of reactions of definite velocities, *b*) that these velocities are *ceteris paribus* proportional to the absolute quantities of the genes, *c*) that the series of turning points are points of intersection of the curves of the two reactions, and *d*) that therefore the position in time of these points of intersection is a simple function of the proportion of the two quantities of the genes in question. It should be emphasized that every criticism of these conclusions is worthless without a proof that either the underlying facts are not correct or that other and better conclusions can be drawn from the facts.

Here then has been derived for one type of genes, the sex-genes, a definite idea of their action: the production of chains of reaction of definite velocities which are a function of the quantity of the gene in question. As early as 1917 the present writer, after having studied another case, which led to the same conclusions, had enlarged them to apply to all genes. In '20b and '27a he used this insight as the basis for developing a general theory of heredity, a theory which has been called by some critics the beginning of a new era in genetics and by others bunkum, neither sound genetics nor sound physiology; a reception which in view of historical parallels seems rather encouraging to the author. But this generalized theory may be dismissed here and only such material reviewed as furnishes further evidence on the nature and action of the gene.

2. *Multiple allelomorphism*

The different sex genes of the races of the gipsy moth behave genetically like multiple allelomorphs; our work therefore demonstrated for the first time that a series of multiple allelomorphs of a definite gene was really a series of different quantities of this gene. There is a possibility that sex-genes are different from other genes; discarding this the present writer came to the conclusion ('17, '20b, '24) that most if not all multiple allelomorphs are of the same order. Two ways of proving this generalization were visible, first the indirect way of demonstrating that as in the case of intersexuality series of multiple allelomorphs were linked up with reactions of definite velocities, and second the direct way of proving the quantitative nature of multiple allelomorphs. The first line of demonstration was followed by the present writer in his work on the markings of gipsy-moth caterpillars ('17, '20b, '24), after Sewall Wright had come very near to the same result in his work on rodents ('16, '25). A similar demonstration for non-multiple allelomorphic genes was given recently by Ford and Huxley ('27). The second direct way of approach has only recently been made possible through the brilliant work of Sturtevant on the bar series of *Drosophila* ('25).

Wright studied a multiple allelomorphic series of a diluting gene for coat and eye color, which may be combined with different factorial constitutions of other genes and produces in these combinations closely parallel series of effects. This leads him to the conclusion (Wright in Castle and Wright, 1916, p. 71) that "it seems most satisfactory to attempt to explain the results on the basis of four quantitative gradations of one factor, which determines the amount of the basic color-producing enzyme." In a recent publication ('25) the same author returns to this subject and concludes "that the factors of the albino series determine the rate of some one process fundamental to all pigmentation . . . . ." The experiments of the present writer, which have led to the actual demonstration of such curves of velocity in a parallel case, have been overlooked by this author, which makes his work still more important as a verification of our conclusions.

This work of the present writer ('17, '20b, '24) has enabled him to study the effects of a multiple-allelomorphic series of a gene on a character in different stages of development. The characters in question are the markings of the caterpillars in different geographic races of the gipsy-moth, characters which can be traced through the different stages of development of the caterpillars. From the manifold facts which the study of the races and their crosses has brought to light only those pertaining to the present question may be mentioned. The two extreme races are that with light-marked caterpillars, retaining their pattern throughout life up to the last instar, and a darkly pigmented race not exhibiting the pattern of light markings. Between these stand other races which in young stages show the light pattern, which however is covered in the course of development with dark pigment so that grown up caterpillars of such races cannot be distinguished from those of the dark pigmented races. We might call this the intermediate type. Between this and the dark races as well as the light ones many other races are found showing the same type of developmental change from light to dark but in different degrees. Light and dark are a simple pair of allelomorphs and all the other intermediate types are based on multiple allelomorphs of these genes. This is not surprising as we know that in the silk worm also many types of markings form such allelomorphic series. If now a light race is crossed with a dark one the F_1 caterpillars are light in young stages and become dark in later stages of development, thus behaving exactly like the pure intermediate races. If we plot curves of the changes of pigmentation during development in the different pure races, dividing the scale from light markings to no markings into classes we get empirical curves of the progress with time of pigment deposition in the skin of the larvae. If this more or less increasing deposition of pigment is the result of a chain of reactions, these curves demonstrate the typical velocities of the reaction. (For details see the full presentation in '24). If these empirical curves are plotted for the pure races as well as their hybrids we realize at once that the different multiple allelomorphs of the pigmentation factor have the effect of producing pigmentation curves of different and specific velocities, the velocities of hybrids lying between those of the respective pure races. Here then we have first the exact demonstration that such different states of a gene, which are called multiple allelomorphs, produce reactions of different and typical velocities; further a very strong intimation that these multiple allelomorphic genes are different quantities of the same gene, as

otherwise it could hardly be understood that hybrids between light and dark races have the same curve as pure intermediate races (The effect of the allelomorphs $AiAi$ = effect of $Ad + Al$).

The work of Ford and Huxley ('27) does not deal with multiple allelomorphs but with ordinary genes controlling eye-color in *Gammarus*. But as eye colors in other animals (*Drosophila*) furnish typical examples of multiple allelomorphism it might be quoted at this point. The authors found in *Gammarus chevreuxi* races with different rates of velocity in regard to the darkening of eye-pigment, as shown in empirical curves. It was shown that the hereditary difference of the two races was that of a simple Mendelian gene, thus demonstrating that certain genes are causing definite rates of reaction. In this case there was no way visible to connect the different rates of the specific developmental process with different gene quantities. On bringing together facts of this type with such ones as reviewed before the present author has been led to consider whether or not the majority of mutations consist in changes of the typical quantity of the gene ('17, '20b, '23a, '27a).

As mentioned before a direct demonstration that multiple allelomorphs are in fact different quantities of the same gene can be found in Sturtevant's ('26) work on the bar eye of *Drosophila*. It is known that bar is a dominant mutation from normal, reducing the number of facets. A further reduction was found by Zeleny in his mutation ultrabar, which behaved genetically as a multiple allelomorph to bar and normal. Sturtevant however proved in a series of exceedingly beautiful experiments that ultrabar is the product of unequal crossing-over resulting in the location of two bar genes in one chromosome. Thus he was able to build up individuals with 1, 2, 3 and 4 such bar genes and to study the effects on facet number. He further found another mutation in the bar series, infrabar, having an intermediate effect between normal and bar. But this gene has some special features in regard to the phenotypical effect as well as in its behavior in temperature experiments. Therefore Sturtevant does not consider it as a member of the otherwise quantitative series. The present writer is of different opinion, but for the present purposes a discussion of this point might as well be left out of consideration. Here then we have a series of genotypes behaving experimentally like multiple allelomorphs. But it is an experimental fact that the majority of the members of the series are formed by different quantities of a gene. This series is linked with a series of facet numbers exactly parallel to these quantities. An analysis of the following tables computed from Sturtevant's data will illustrate our point. If B is the gene for normal, B_1 for infrabar, B_2 for bar the combinations shown in table 1, page 313, have been produced.

We can arrange this table so that the different possible types of heterozygous forms parallel the respective homozygous forms and get the table (the numbering of the combinations is the same as in the first table), shown in table 2, page 313.

This table seems to the present writer very impressive. With the single exception of No. 13 all the heterozygous combinations closely parallel the homozygous series in regard to decreasing numbers of facets. Sturtevant has now proved conclusively that No. 4 has four quantities of the gene B_1, No. 5 two quantities of B_1 and B_2 each, No. 6 four quantities of B_2, etc. This series 1 to 6 affects increasingly the number of facets in negative order. Among the members

TABLE 1

NUMBER	HOMOZYGOUS formula	HOMOZYGOUS phenotype	FACETS	NUMBER	HETEROZYGOUS formula	HETEROZYGOUS phenotype	FACETS
1	$\frac{B}{B}$	normal	779.4	7	$\frac{B}{B_1}$	normal-infrabar	716.4
2	$\frac{B_1}{B_1}$	infrabar	320.4	8	$\frac{B}{B_2}$	normal-bar	358.4
3	$\frac{B_2}{B_2}$	bar	68.1	9	$\frac{B}{B_1B_1}$	normal-doubleinfrabar	200.2
4	$\frac{B_1B_1}{B_1B_1}$	double infrabar	38.2	10	$\frac{B}{B_1B_2}$	normal-barinfrabar	50.5
5	$\frac{B_1B_2}{B_1B_2}$	barinfrabar	26.7	11	$\frac{B}{B_2B_2}$	normal-ultrabar	45.4
6	$\frac{B_2B_2}{B_2B_2}$	double ultrabar	24.1	12	$\frac{B_1}{B_2}$	infrabar-bar	73.5
				13	$\frac{B_1}{B_1B_1}$	infrabar-doubleinfrabar	138±
				14	$\frac{B_1}{B_1B_2}$	infrabar-barinfrabar	37.8
				15	$\frac{B_1}{B_2B_2}$	infrabar-ultrabar	41.8
				16	$\frac{B_2}{B_1B_1}$	bar-doubleinfrabar	38.3
				17	$\frac{B_2}{B_1B_2}$	bar-barinfrabar	37
				18	$\frac{B_2}{B_2B_2}$	bar-ultrabar	36.4
				19	$\frac{B_1B_1}{B_1B_2}$	doubleinfrabar-barinfrabar	27.9
				20	$\frac{B_1B_1}{B_2B_2}$	doubleinfrabar-ultrabar	26.7
				21	$\frac{B_1B_2}{B_2B_2}$	barinfrabar-ultrabar	24.1

TABLE 2

HOMOZYGOUS Number	HOMOZYGOUS Facets	HETEROZYGOUS WITH B Number	HETEROZYGOUS WITH B Facets	HETEROZYGOUS WITH B_1 Number	HETEROZYGOUS WITH B_1 Facets	HETEROZYGOUS WITH B_2 Number	HETEROZYGOUS WITH B_2 Facets
1	779.4	7	716.4	7	716.4	8	358.4
2	320.4	8	358.4	12	73.5	12	73.5
3	68.1	9	200.2	13	138±	16	38.3
4	38.2	10	50.5	14	37.8	17	37
5	20.7	11	45.4	15	41.8	18	36.4
6	24.1						

HETEROZYGOUS WITH B_1B_1 Number	HETEROZYGOUS WITH B_1B_1 Facets	HETEROZYGOUS WITH B_1B_2 Number	HETEROZYGOUS WITH B_1B_2 Facets	HETEROZYGOUS WITH B_2B_2 Number	HETEROZYGOUS WITH B_2B_2 Facets
9	200.2	10	50.5	11	45.4
13	138±	14	37.8	15	41.8
16	38.3	17	37	18	36.4
19	27.9	19	27.9	20	26.7
20	26.7	21	24.1	21	24.1

of this series No. 4 is certainly a quantitative condition of B_1, No. 6 of B_2, and No. 5 of B_1 and B_2. Therefore the difference between B_1 and B_2 ought to be quantitative. If this is the case all the possible combinations of 2, 3, 4 quantities of B_1 and B_2 must form parallel series to the homozygous series, which is the case. Finally the gene B with all its combinations falls exactly in line in these different series and therefore must also be regarded as belonging to the series of quantities. In other words, there is a number of different equations involving B, B_1, B_2, which can be solved only if B, B_1, B_2 have typical but different numerical values.

Thus we regard this case as conclusive proof of the quantitative nature of multiple allelomorphs. Our second result was that these different quantities of a gene are linked with reactions proceeding at different rates proportional to the respective quantities which produce the typically different phenotypical result. The present writer has analyzed this case in the same direction and found that the results can best be represented this way. (For details see Goldschmidt, '27a, p. 63 ff. It ought to be mentioned that on p. 68, 69, of the work in question a *lapsus calami* occurred. The tables on these pages have erroneously been calculated as differences instead of as proportions. If corrected the similarity between result and calculation is still better.)

In concluding this section a general point may be mentioned shortly. Many years ago Baur in discussing our views in regard to the quantity of the gene remarked that it is impossible to imagine that the genes are always present in the same quantity. Lillie ('27) has recently taken up the same argument. Speaking of possibilities I might venture the opinion that if chromosomes were invisible bodies and their numerical constancy only deduced from genetic experiments, the same argument would immediately be at hand. The same applies to every numerical constancy in organisms, the segments of insects and the number of cells in the nervous system of *Ascaris*. I cannot see why it is more difficult to conceive a typical number of molecules for a given gene. But finally these considerations are superfluous because it is an actual fact that the effect of a gene is different and typical if present in 1, 2, 3, 4 quantities, which would be hard to account for if the unit quantity was not of fixed magnitude.

B. THE EFFECTS OF THE SAME GENE IN DIFFERENT QUANTITIES IF MORE THAN ONE GENE IS INVOLVED

Genes in different quantities may also be studied in cases of either absence or multiplication of parts of chromosomes, of whole chromosomes, or of whole chromosome sets. In such cases, however, the conclusions are subject to uncontrollable error. The result attributed to different quantities of one gene may be decisively influenced by the corresponding difference in many or all the other genes. If whole chromosomes or even whole chromosome sets are involved the additional effect of the change of the nucleo-plasmic ratio may come into play. Thus experiments of this type can only furnish additional evidence, which has to be handled cautiously, weighing the different possibilities for each case.

The smallest deviation from the single gene evidence is obtained if only a small number of genes are involved, as in the deficiency studies of the Drosophila workers. After Bridges has shown that the effects of the deficiency are of the same order as in the haplo IV, one can safely assume that deficiencies are real absences or at least complete inactivations

of the genes involved. Thus in such cases a gene may be studied in a single quantity in comparison with the double quantity in homozygous condition and the plus or minus-double quantity in normal heterozygous condition. The source of error consists in the presence of a few other genes in the same condition. Bridges noticed first and other writers, notably Mohr, obtained the same result, that characters produced by a single gene, the partner being totally absent, appear exaggerated: characters produced by only one gene *a* differ still more from the normal type than the same characters produced by *aa*. Bridges' explanation of this phenomenon by genic balance is well known. If according to our views the decisive point is the quantity of the gene, an explanation of this phenomenon should be found when multiple allelomorphs are involved in the same experiment. If multiple allelomorphs are different quantities of the same gene complete absence of one gene is to be regarded as the end point of the series. Mohr ('27) was able to study such a series, the well-known white series of eye colors in *Drosophila*, in the case of deficiency. If white, the lowest member of the series, is combined in heterozygous condition with the other members, it has a diluting effect on the phenotype. If the members of the series are combined with deficiency (viz. *Wo*, W_1o, W_2o instead of *Ww*, W_1w, W_2w,) the effect is still further dilution. Total absence of *w* therefore acts like a further still lower member of the series. The present writer feels unable to draw any other conclusions from such facts than that we see here the effects of a different quantity of the gene. In a paper read at the International Genetics Congress, 1927, Mohr produced new facts, which he thinks are in favor of our conclusions.

It is obvious that under these circumstances the phenotypic effect called exaggeration has to be understood in the same way as the effects of other different multiple allelomorphs, namely through the medium of different velocities of reaction. How this can be done in detail has been discussed in the present writer's book ('27a, p. 78 ff.).

The next possibility of studying different quantities of a gene without involving all genes is in trisomic forms as notably given in Blakeslee's work on *Datura* and the triplo-IV form of *Drosophila* (Bridges). Here of course the causes of error are greater, because whole chromosomes are involved with the quantitative disturbance of all their genes and a possible general effect (nucleo-plasmic ratio) in addition. In the case of *Datura* more general results of the trisomic constitution have been studied than effects of the three quantities of individual genes. But in the triplo-IV Drosophilas the effects of three quantities of a gene could be studied. Judging from the case of deficiency and haplo-IV with exaggeration, the respective phenotype in the triplo-IV is expected to be exaggerated in the opposite direction than in the deficiency case, because three quantities of the gene might again be the same as a higher multiple allelomorph. In fact these are Bridges' results, which however are interpreted differently by him, namely by genic balance (see later). At this point a word ought to be inserted about a closely related phenomenon. According to the workers on *Drosophila* many dominant mutations in that form are lethal, when homozygous; homozygous deficiency is lethal; absence of both IV-chromosomes is lethal; on the other hand four IV-chromosomes are also lethal. There is probably a consensus of opinion, that in all these cases some balance in the cooperation of the genes, or expressed more correctly in the effect of the genes,

necessary for normal development is disturbed. It would be difficult to translate this general statement into definite terms without using the idea of definite gene-quantities linked with definite rates of reaction.

A further method of studying genes in different quantities is furnished by cases of polyploidy, especially triploidy and tetraploidy. Here the difficulties of clear conclusions are still greater because all genes are involved and the effect of one of them in three or four quantities will be completely outweighed and a normal balance restored, since the whole system is built up on the basis of such different quantities. There is the additional effect of the nuclear plasmic ratio, which in these cases is a well known fact (see Wettstein's review). Therefore conclusions regarding our problem can hardly be expected, with two exceptions, namely when sex is involved in the triploid intersexes where the presence of the X-chromosome mechanism makes it possible for sex genes to act in different quantities which are not corrected by parallel changes in the quantities of all the other genes; and further when in triploid hybrids the phenomenon of dominance is involved. That triploid intersexuality leads indeed to the same conclusions in regard to the sex-genes and their action as diploid intersexuality has been repeatedly shown by the present writer ('23, '25, '27). The case of dominance will be discussed later.

C. EVIDENCE DERIVED FROM THE STUDY OF THE EFFECTS OF EXTERNAL CONDITIONS UPON THE PHENOTYPICAL EFFECT OF A GENE

Thus far we have reviewed the evidence furnished by the study of genes in different quantities. Another method of attacking the problem is the study of the action of particular genes under different environments. The first definite information from experiments made with this end in view, was found in the present writer's experiments with intersexes. If the results of his analysis of the phenomenon of intersexuality are correct, namely that intersexuality is produced if the two simultaneous chains of reaction, those of female and male differentiation, have a point of intersection during development, it follows that intersexuality could be produced within normal genic constitution, if such a point of intersection could be induced experimentally. The only visible method for such an experiment was the use of low temperatures, on the supposition that the sex-differentiating reactions and the other reactions controlling rate of development might have a different temperature coefficient. Such experiments were performed many times, always with positive result. ('21). As a matter of fact Kosminsky ('09) had already performed the same experiment with the same result without knowledge of intersexuality and all the questions discussed here, and has since enlarged his former results ('24). One further consequence (which Prof. J. Huxley kindly suggested) is that similar experiments performed with intersexual stock must shift the degree of intersexuality towards higher intersexuality. This experiment was also performed successfully.

These experiments led to a very important conclusion: The effects of temperature (or other experimental conditions) may be phenotypically identical with the effect of a different gene, the reason being that in both cases the rate of a definite reaction is changed, in the same sense. This consideration furnished a simple explanation for ('20b) such phenomena as e.g. the phenotypic identity of heritable geographic forms with forms produced in temperature experiments on butterflies

in the classic researches of Dorfmeister, Standfuss, Merrifield, Weismann; or for the behavior of seasonal-dimorphic butterflies, as has been discussed in detail by the present writer ('17, '20b, '23c, '27a) and controlled experimentally by his former student Süffert ('24); or further for the many instances of phenotypic identity of modifications and mutations. For our present discussion, however, the important point is the demonstration that definite genes are really connected with definite rates of reaction.

There have since appeared other investigations which in our opinion lead to the same result. We mention first Zeleny's ('23) work on the influence of temperature upon the bar eye in *Drosophila*. This author concludes from his experiments: "Perhaps the most interesting point in connection with the present data is the demonstration that they furnish of the fact that the gene ultrabar has the same type of reaction as a temperature difference. It is possible to state the effectiveness of particular germinal factors in terms of the corresponding effects of temperature." And further: "In view of the fact that temperature is effective only during a few hours of larval life, it may be considered that the initial steps in the formation of ommatidia are confined to a definite embryological period. (This applies also to the butterfly wing. R. G.) The length of this period is determined by the general physiological processes of the larva, while the rate of formation of ommatidia during the period is a function of special processes, which have a different coefficient." The present writer thinks that with the introduction of the conception of velocities of reaction into Zeleny's results they fall completely into line with his conclusions. In addition we recall that it has been shown for the bar-genes with which Zeleny worked that it is their quantity which counts.

A very remarkable piece of work which leads in the same direction has been done by Plunkett ('26). He studied the effects of temperature upon bristles in *Drosophila*, trying to exclude all disturbing factors. The results—mainly a consistent reduction of bristle number with increasing temperature—were minutely analyzed. Some of his conclusions are: The essential difference between the dichaete and wild-type flies (so far as bristles are concerned) is the velocity of a bristle-reducing reaction. The effect of this continuous reaction, namely bristle or no bristle, takes place if the concentration of the produced substance equals or exceeds a certain threshold value. The action of the gene, then, is the production of a chain of reactions, namely: the gene produces from a protoplasmic component, the distribution of which means localization, a catalyst *R*, the concentration of which is typical for the respective gene. For this production of *R* the gene itself may be the catalyst. The concentration of *R* is again proportional to the velocity of a reaction, the already mentioned reaction for the production of bristles, conceived as decomposition of a thermolabile bristle-forming catalyst *B*. Here then we have again all the elements of the present writer's old conception of the action of the gene by definite velocities of reactions, producing the formative substances. But there is one difference: not the quantity of the gene but the quantity (concentration) of a product of the gene, the catalyst *R*, is linked with the different velocities. We have seen already that ample proof is existant to show that the quantity of the gene itself is decisive, whatever the intermediate points of the chain or reactions might be. Thus Plunkett's work, as far as it goes, confirms the present writer's former conclusions. It might be added that Plunkett draws general conclusions from his analysis

which are indeed a restatement of the present writer's ('17, '20b, etc.) views (unknown to the author), e.g. "It is a tenable hypothesis that this is the way in which all genes produce their observed effects: by differential acceleration of various reactions in the organism" or "In such a complex system of successive and 'competing' reactions the differential acceleration of certain ones can produce great, and apparently complete differences in the end results. It is not at all impossible that the metabolic and morphogenetic differences among species, individuals and tissues may be entirely due to differential acceleration, by specific catalysts, of the infinite variety of 'spontaneous' reactions possible to the components of protoplasm." Readers of our papers (notably '20b and '22a) will be familiar with these conclusions, even to the expression "competing reactions." One of the writer's papers ('23c) is entitled "Contributions to the theory of differentially accelerated reactions" (literally "tuned reaction-velocities"). It is further remarkable that proceeding in his analysis Plunkett comes to views regarding the relation of these genic reactions to morphological localizations, approaching very closely those which the present author developed in his book, which was through press when Plunkett's paper appeared. This encourages the present writer to believe that after all his theory of heredity is "sound genetics and sound physiology."

D. EVIDENCE DERIVED FROM THE STUDY OF DEVELOPMENT OF MENDELIAN CHARACTERS

In reviewing the case of multiple allelomorphs for the pigmentation of *Lymantria* we have already met with the study of Mendelian characters during development. A number of other facts are known, which furnish further insight into the mode of action of the gene. Two students of Haecker (who introduced for this type of study the term phenogenetics) Pernitzsch and Schnakenbek ('13) showed that the difference between normal and albinotic axolotls is mainly a result of different rates of growth and multiplication of the melanophores and xanthophores. The present writer ('20, '23c) found that the differently colored parts of the pattern of a butterfly wing are the product of different rates of differentiation of the scales, with the effect that the scales in different parts of the pattern are ready for the deposition of pigments at different times. This demonstrated the presence of a series of differently timed reactions working together in a definite way (see detailed discussion, '27a). In a paper on the color-types of the fish *Oryzias* Goodrich ('27) finds that the different Mendelian phenotypes are produced by deposition of different quantities of pigment in given numbers of cells. This might of course be expressed in terms of reaction velocities.

In this section such general studies on development might also be mentioned as do not relate to definite genes but rather to the general unanalyzed genotype. We think of the work of Stockard, Newman, Harrison, Spemann, Brandt. Here many instances are found demonstrating the importance of timed reaction-velocities in connection with the genotypic constitution. (For particulars and discussion see Goldschmidt, '27a.)

E. EVIDENCE DERIVED FROM HETEROZYGOSITY

There is, I believe, a consensus of opinion that dominance is not a property of an individual gene but one of the results of the interaction of the genes, including the one in question, in producing the

visible character during development. In trying to formulate an opinion about the production of this phenomenon two primary possibilities are given. The dominant and the recessive gene might act independently, the result being determined by some resultant of both actions. It is evident that in this case the phenomenon ought to be explained on the same basis as the phenomenon of epistasis. For this we have shown in a special case, namely the competing reactions produced by the sex-genes, that the result depends upon the two respective velocities of the competing reactions and a third variable, an independently determined point in development, determined by some or many other genes. In this case the dominant and recessive, or the two epistatic genes, might differ qualitatively or quantitatively. In any case the phenomenon of dominance or epistasis can be understood only on the basis of a set of differential reactions of definite velocities (for details see Goldschmidt, '27a). The second possibility is that in the heterozygote the dominant and the recessive gene do not act independently. If we assume the difference between these two genes to be one of quantity, this would mean that, e.g., the allelomorphs of the respective quantities 10 and 6 would have a single combined action based on the quantity 16. In our experiments on intersexuality we have produced experimental proofs (see '23b, '25a and much unpublished material) that actually this is the case if two different quantities of an allelomorph are combined (male intersexes built up from three races). If the same applies also to other cases dominance and its different degrees would result from a system of reactions where one, with its specific velocity, is the product of the combined action of the added quantities of the two allelomorphs, the others being determined by the other genes controlling the exactly timed reactions necessary for development. How such systems work is discussed in Goldschmidt, '27a, p. 67 ff. Here the argument is also applied to such cases as the dominance within the bar eye series of *Drosophila*. It seems therefore to the present writer that the phenomenon of dominance lends further support to the idea that genes are connected with timed chains of reactions proportional to their quantities. In harmony with this interpretation are the facts known about the results of the combination of two recessives with one dominant gene (Correns, Wettstein, Bridges, Morgan). In some cases two recessives dominate one dominant; in others the opposite is true. It seems difficult to explain such facts without assumptions of the foregoing type.

There might be mentioned also the phenomenon of change of dominance during individual life. The present writer ('17, '20b, '24) first analyzed such a case genetically in the already quoted work on the pigmentation of caterpillars. In F_1 between a light and a dark race young caterpillars are light and change later towards the dark side. The study of the pigmentation curves in such cases showed that the facts have to be explained on the basis of typical curves of reaction of definite velocities in the parents and intermediate velocity in the hybrid. The phenomenon then again supports the general idea. Honing ('27) and Ford and Huxley ('27) have since analyzed similar cases and accepted our explanation.

F. THE CASES OF VARIEGATION

In recent genetic literature the study of a certain type of variegation has aroused great interest and has been used as a starting point for conclusions upon the nature of the gene. Speaking generally these varie-

gations are produced on the basis of a single Mendelian unit. In appearance they show "a continuous series of quantitative variations ranging from apparently deep self colors with only occasional color changes that are apparent through a series of dilute self-colors with all gradations of color from deep red to whitish and with increasing numbers of dots, splashes, lines, bands and larger segments of darker and lighter colors; and through a series of variegations varying in pattern from very heavy to extremely light." This description by Eyster ('28) of the pericarp case in maize covers also the more or less similar types in other cases, viz. *Antirrhinum*, *Mirabilis*, *Capsella*, etc. These unstable types are not confined to different individuals but occur within the same individual. It has therefore to be explained why on the basis of an apparently single Mendelian gene a complex mosaic is produced with a number of typical features. The first idea is that there is something unusual the matter with the gene in question, Correns ('19) directly speaking of a sick gene. All explanations which have been tried, though looking at first sight very different, are of much the same order if viewed from some distance. All interpretations agree that something happens to the gene in question so that different cells are produced and the stage of development in which this something occurs determines the resulting pattern. The event in question is regarded by Emerson ('13, '17, '22) as a temporary inactivation of the gene. Baur ('24) also does not wish to touch the old conception of the gene as the genetic unit. But realizing that some diversity of the genic basis is needed to explain the facts he assumes that a number of unilocal genes are present which recombine in different ways. Correns ('19) was the first to make the revolutionary step of explaining the facts by assumptions regarding the finer structure of the gene. He writes:

> "In order to have at least a model one might assume that the gene consists of a large molecule to which the same sidechain of atoms is attached, say, ten times. This number might be mutable, might undergo changes in the plus or minus direction under unknown conditions 'external' for the gene. To each number of these sidechains would correspond a definite ratio of white and green in the mosaic plant . . . . . The difference in this interpretation . . . . . would be that the state of the gene, the number of sidechains, attached to the gene molecule, is not constant, but that new chains could be added or old ones detached, and this during ontogenesis of the individuals."

Here then we have already a somewhat quantitative conception based on the assumption of a complex structure of a gene which may change quantitatively in regard to definite parts of the whole. A step further leads to the theory of Anderson and Eyster ('24, '25, '28). The last named author assumes that the facts can only be explained if a quantitative segregation of parts of the gene takes place in development. The gene, then, is regarded as composed of a constant number of genomeres or gene elements, which may or may not be chemically identical. The genetic difference between pigmented and pigmentless forms is given in the genomeres, the genomere *C* being mutated into *c;* both genes contain the same number of genomeres, either *C* or *c*. If, however, only a certain number of genomeres mutate from *C* to *c* an unstable gene with two types of genomeres is produced, the gene of the variegated forms. This gene may be divided into its genomeres during somatic mitosis, giving different combinations of genomeres up to a complete separation of the two types *C* and *c*. It is clear that all the facts can be represented by this conception, which is very closely akin to that of Correns.

If we compare these different concep-

tions of Baur, Correns, and Eyster we see at once that all of them start from the necessity, derived from the experiments, of introducing some quantitative element into the conception of the gene in order to have a chance of sorting out such quantities. Baur prefers a definite quantity of different unilocal genes, Correns accepts a definite quantity of permutable side chains, and Eyster believes in permutable quantities of different genomeres. The reader of the present writer's work will at once realize how much these assumptions may be simplified and brought in line with all our other knowledge of the gene if the unilocal genes, sidechains and genomeres are replaced by molecules (or group of molecules) of the substance called a gene. If, as we believe we have proved, one of the essential properties of the gene is its quantity, the situation is the following: The "pigmented" gene has a definite quantity, say ten molecules. The mutation to pigmentless consists in changing this quantity into four molecules. Normal, stable genes have the elementary property of being "adsorbed" in the chromosome, always in their characteristic quantity, at least in all cells up to the point of their final determination. Unstable genes, properly called by Correns sick genes, lack something in their physico-chemical properties necessary for constancy in their number of molecules. In mitosis therefore the twenty molecules present at the time of fission of the chromosomes may be "adsorbed" by the two daughter chromosomes say as 12 and 8. It is not necessary to work this out in detail: The result must necessarily be the same as in the other hypotheses. The advantage is, besides the fitting into the general theory of the gene, that no different types of genes or genomeres with quantitive assortment are needed but simply the definite quantities of the one gene substance reckoned in numbers of molecules (or molecule-compounds). Thus the facts about unstable genes seem to add new material to the already broad basis of our general conclusions.

G. THE NATURE OF THE GENE

There are no direct facts giving information about the nature of the gene. If our conception is correct that the gene is a definite quantity of something (of course qualitatively different things in many different genes) linked with a chain of reactions with a velocity proportional *ceteris paribus* to its quantity, it does not single out a definite type of chemical substance. However all general considerations have led practically everybody who discussed the problem since Driesch in premendelian days and Hagedoorn in early Mendelian days to regard the gene as a type of enzyme and specifically as an autocatalyst. The present writer has also joined this view, the only alternative to which is at present agnosticism. Of course this gives no information about the members of the chain of reactions catalysed by the gene. If Plunkett (1926), for example, concludes from his experiments "that the gene acts as a true catalyst" which as the first step in the chain of reactions catalyses the production of another catalyst, which in its turn is connected with further reactions of definite rate, this is not a different view from ours, as Morgan ('26) seems to believe, but a specification of a more general assumption. Further discussion of this point does not seem profitable at present.

H. THE INTERACTION OF GENES IN DEVELOPMENT

If we try to formulate definite ideas regarding the gene and its mode of action we do it with the end in view of understanding the rôle of the genes in directing

typical development. It is therefore not surprising that the present writer tried to enlarge the conception of the gene and its action, which he regards as proven by experiment, into a general theory of heredity ('17, '20b, '27a). The general basis of this is the conception of differential and balanced (*abgestimmte*) reaction velocities. We have seen already that Plunkett's work led him to accept this conclusion. The present writer has further tried ('27a) to work out in detail this general conception and to apply it to the details of development as analysed in experimental embryology. Studying the facts in the light of the basic conception he arrived at a consistent and simple theory of heredity, which brings together the facts of genetics as well as of experimental and descriptive embryology. This theory, which certainly goes beyond the arbitrary limits set by some to "sound" genetics and to "sound" physiology, will not be reviewed here. But it might at least be compared briefly with the only other attack on the problem, Bridges' conception, not yet elaborated, of the genic balance. This will be of special interest because the type of facts (intersexuality) and the type of explanation (balance of sex-genes) from which Bridges and the present writer started was identical. Bridges' idea will best be presented in his own words ('22):

"Each gene is essentially a factory which is manufacturing a characteristic set of chemical products that are delivered to the common cytoplasm, and that produce development through interaction with each other and with materials from outside. But since the chemicals produced by the different genes are different, some genes will have much effect upon one character and little effect upon another, so that a relatively small proportion of the genes will be actively concerned in producing any given character. Some of these genes tend to make the character more pronounced and others tend to make it less pronounced, so that the grade of development actually realized by each particular character will be determined by the equilibrium between its modifying genes. The forms into which a given character can be modified are in general quite diverse, but for the sake of simplicity we may call them all + or − modifications. If the effectiveness of a given + or − modifier is changed by mutation, the grade of the character will shift correspondingly."

This statement is rather general and it will hardly be possible to account for orderly development without substituting some concrete conception for the generalities. When we read that "the grade of development actually realized by each particular character will be determined by the equilibrium between its modifying genes" we see at once, I believe, that this statement is endowed with a concrete meaning only if we make the step from the balanced genes to the balance of the action of the genes. Such a balance however, working in development, can hardly be conceived otherwise than in the form of balanced rates, of a harmony of timed chains of reactions, playing together in an orderly, balanced, properly tuned way. In other words, the conception of genic balance, if interpreted in concrete terms, leads to our theory of balanced action of the gene.

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SUB-HUMAN CULTURE BEGINNINGS

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As ONE of the social sciences, Anthropology deals with that relatively closed system of phenomena called culture. This system is closed in the sense that life is a closed system. The biologist does not repudiate the results of physics and chemistry; but his task is with phenomena and problems on the specific level of life. He expects that his findings will ultimately be convertible into findings in terms of the inorganic sciences, yet he realizes that his approach must be in terms of his own. Just so the social scientist does not assert that human social activities are controlled by a metaphysical something unrelated to organic forces. But he does believe that the first explanation of cultural phenomena must be in cultural terms. He sees every cultural phenomenon preceded by other phenomena and related to them; and this relation, on a cultural or social or supra-organic level, he feels must first be clarified and intellectually organized. Only then can the approach from the organic or physiologic level, and still later that from the chemical one, lead to fruitful results. Anything else leads to short-circuiting of understanding.

THE ORGANIC BASIS OF CULTURE

Within the social sciences, history, economics, politics deal with only part of the totality of culture manifestations. They are, therefore, essentially restricted to consideration of phenomena which lie wholly within the system of culture. These are purely social sciences. Anthropology has a somewhat different outlook. So far as it concerns itself with races, with human beings respectively set apart and united into groups by a common heredity, Anthropology is organic or natural science. So far as it examines institutions, customs, folk-ways, inventions, and speech, it is supra-organic or cultural. By common consent the study of the earliest and most backward peoples and cultures has been left to Anthropology. The significance of these incipient cultures is obviously not so much intrinsic as in the light which they may shed by enabling a wider and fuller range of comparisons on the nature of culture as a whole. The relation of the system of culture to the organic system is thereby thrust into the foreground. I have on another occasion defined the special sphere of Anthropology as being concerned with the interrelation of the organic and the cultural. I have also been criticised, perhaps justly, for abandoning the program after formulating it. The reasons were the obvious one of difficulty and the present slender promise of productive results. It is however now and then worthwhile to envisage the larger problems which in candor we must admit to be still largely insoluble, in order that our daily work as scientists may remain as much as possible in touch with the fundamentals of science, and not degenerate

into routine. This is my apology for venturing upon a subject in which as yet it seems impossible to be definite without remaining cautiously narrow, and in which on the other hand one can not be broad without becoming indefinite. This subject is: the organic basis and origin of culture.

There are three principal approaches to the question of the origin, or original nature, of culture. These are, first, the prehistoric or archaeological record; second, ontogenetic development in the infantile human individual; and third, comparison with those of the infra-human animals most likely to manifest anticipations of cultural activity.

The archaeological approach has the virtue of giving us, so far as it goes, an objective mass of evidence. It is further advantaged in that its phenomena occur associated in nature with geological and paleontological phenomena, so that they can be arranged with considerable certainty in an order of time which is objectively founded. The archaeological method, however, suffers from the fact that its data are primarily tangible, whereas much of culture, in one aspect its very essence, is intangible. Archaeology recovers some of the tools, materials, and mechanical processes of the past; but we can only conjecture the thoughts and institutions and human relations which accompanied these tools and processes.

The ontogenetic approach—child study —is full of promise. But scientific recording in it has been almost as scant as recognition of the promise held by further data has been wide-spread. We have hardly got beyond the stage of realizing that the first necessity is to rid ourselves of a mass of implicit but confusing interpretations that block progress. In this clearing of the ground the Behaviorist school of psychologists have done valuable work. Too often, however, they have acted as though this first step were also the final one. And whatever their own attitude, they have certainly helped create the impression that human beings come into the world with practically no equipment. This, if true, would make the acquisition of culture by each individual almost entirely a matter of life experience in contact with other individuals already possessing culture. Carried to its logical conclusion, such an interpretation would pull the organic basis out from under culture, while at the same time dealing with it not as a system in itself, but as a series of accidental events. The Behaviorists are evidently far more interested in method than in results; indeed pride themselves on the fact. What they cannot rigorously prove they will have nothing to do with; and too largely the outcome is an attitude as if what they prefer not to operate with did not exist.

The comparative approach through examination of infra-human behavior also has its limitations. It is again a difficult field, in which controlled facts are scarce, and misinterpretations easy, especially those of the anthropomorphizing kind. Domesticated animals must of course be used with caution. They have not acquired culture, but they have come under its influence. The most highly socialized organisms, sometimes presenting astounding analogies to the human societies which carry culture, occur among the insects, a group differing thoroughly in structure, and apparently in the nature of their reactions, from ourselves. The upshot of the work of the most critical students in the field, such as Wheeler, seems to be a stressing of the essential difference between insect and human societies, a pointing out that the similarities are analogies and not realities.

THE BEHAVIOR OF APES

Fortunately, however, the last fifteen years have seen a burst of interest in those of the mammals most nearly related to ourselves, the Primates, and among the Primates in the anthropoid or man-like apes. This interest has been partly popular, but has also been reflected in the endeavors of biologists and psychologists to secure reliable evidence and a sound understanding of the behavior of these apes. The work of Koehler, Kohts, Boutan, Yerkes, Furness, has been as critical as is possible in the present development of science. Controlled experiments have been added to systematic observations. Strangely enough, not one of the studies of the great apes has been made by an anthropologist. But there is in this at least the advantage that an anthropological interpretation cannot be challenged on the ground of bias or preconception.

All of the four types of man-like apes have been studied, but the chimpanzee has provoked most interest. The gibbon is very different from ourselves in proportions and behavior; he is thoroughly arboreal. The orang approaches him in this respect; he possesses a sluggish and melancholy temperament. The gorilla, perhaps anatomically closest to man, has been difficult to capture and keep in confinement. His study has yielded some results; but his attitude toward human beings is aloof. The chimpanzee is about equally similar to man, shows definite responsiveness to human association, and is relatively hardy and docile.

THE CHIMPANZEE

The chimpanzee's life is primarily terrestrial, although he is a splendid climber. The body is not carried fully erect, and the knuckles frequently touch the ground in walking; but locomotion is on two feet. The differentiation of the limbs into a locomotory and a manipulative pair is not as marked as in man, but approaches it. There are few if any human manual abilities which the chimpanzee does not possess. He is endowed with much greater strength. The available data suggest that his muscular power may be estimated at three times our own.

The infant chimpanzee begins to teethe within two months, walks at the end of six, has all its milk teeth within twelve months, and possesses at that age sufficient muscular coördination to secure for itself part of its food, although it may continue to nurse. A period of playfulness and activity follows. Growth is at first slower than in man, but rapid toward adolescence. Sexual maturity comes at about eight to ten years in females and ten to twelve in males. Accompanying sexual maturity there is a change of temperament. Playfulness diminishes, indolence and irritability increase, the individual becomes less exuberant in his manifestations of sociability, and, on account of his great strength, somewhat dangerous. This appears to be part of a wider process involving a slowing down or at least change in direction of what we call intelligence. In experiments, young chimpanzees have made the best performances. The one adult female of Koehler, for instance, was rated by him near the bottom of his list of seven immature chimpanzees. A human parallel is obvious. The duration of chimpanzee life is not known, but is estimated at not very much less than that of man.

CHIMPANZEE PSYCHOLOGY

The senses of the chimpanzee are similar to our own. Sight, which is the easiest to test in both species, is much alike in perception of color, form, and distance.

Hearing appears to be about as acute as in man. Taste and smell are utilized very much as by ourselves, primarily with reference to food. All in all, the sensory equipment is definitely analogous to that of man, and different from that of sub-primate mammals.

This is expectable. A body like ours with senses like those of a dog is a combination hardly to be anticipated in nature. The chimpanzee's use of his senses is also human. If he sees something out of his reach but with a string attached to it, he pulls the string with as little hesitation as a human being. If there are several strings, he draws the one lying in most direct line toward himself; or if only one is actually in visual contact with the desired object, he pulls that one. After all, he possesses a string-pulling mechanism—arms and hands and fingers; and this would serve him in little stead if he saw blurred instead of clearly, or if his ability to interpret spatially were deficient.

If food is put on the ground outside a barred window, a string attached to it and led indoors, and an ape allowed to survey the situation, he quickly hauls the food up on the cord. A dog fails to grasp the situation. He may starve before he takes the cord in his mouth and backs across the room to haul the food in. He does not see the relation of food, string, and himself; he cannot connect or synthesize them.

Tests in which an animal is put under conditions where it makes a selection between several possible acts but is compelled to defer action on the choice, have yielded in the rat a memory span of a few seconds; in the dog, a few minutes; in the ape, according to Kohts, a quarter of an hour, and, according to statements of Yerkes, under favorable conditions several hours. In the human being the range varies from a few minutes in a small child to years or the entire life in adults. But such deferred choices have something artificial about them. Rats do not encounter swinging doors and electric flashlights in nature. The memory span of mammals may be indefinitely long for places, persons, and experiences. What the experiments seem essentially to show is that sub-human animals all make poor showings in tests, the dog slightly surpassing the rat, and the chimpanzee the dog. Laboratory tests are after all devised in culture primarily for organisms that have culture. We may simplify them and yet make them extremely difficult for an organism constructed differently from ourselves. They tend to be weighted humanly, whether we want it or not.

As regards imitativeness, observations are at variance. Koehler interprets the chimpanzee as much less imitative than does Yerkes. But the latter found a gorilla non-imitative almost to the point of being negatively suggestible. This, however, was with reference to use of appliances or solution of problems such as the animal would not encounter in nature. When it came to eating new foods, the gorilla was willing to follow example—provided no persuasion was applied and it could withdraw to make the test in seclusion. Emotional factors are evidently of the greatest influence as regards imitativeness; and these are conditioned by the social relations in which the ape finds itself. Yerkes' orang and chimpanzees were almost members of his household. Koehler's apes lived primarily in a colony of their own. It is clear that they learned very little from one another in the solution of posed problems. Imitativeness is evidently called out largely by association with human culture.

LACK OF SPEECH AMONG APES

On the side of speech it is agreed that the ape is completely deficient in imitativeness. Observations and experiments are uniformly negative. At this point the close human associations and manual adaptations of Yerkes' animals are of high significance. They did learn to brush their teeth, to spit, to eat with a spoon, to go to bed, and a hundred other things which the family was doing. They could not be taught to speak at all.

Furness, by long and repeated practice, taught his young orang to say "Papa," and apparently to realize that this sound complex in some way related to her master. Whether the animal recognized that "Papa" was Furness' name, as Furness believes, is another question. When he goes on to tell how the animal, as she was being carried into water which she dreaded, clung to him and cried "Papa! Papa! Papa!", the facts may be accepted, and yet the interpretation that the ejaculation was an "appeal" in the human sense is wholly subjective. Next, the same orang was taught to pronounce the word "cup." Her tongue was repeatedly pressed back with a spatula into position for articulation of the hard "c" or "k" sound. After she had learned to release the consonant and the vowel, the lip motion of the "p" was added and mastered. The poor brute managed after a time to produce a pretty fair rendition of the word "cup." But there is nothing to show that it meant anything to her. Pronunciation may have seemed nothing more than an end in itself; perhaps a game, or an intrinsically meritorious act that earned approval. Once at night, on awakening, she spontaneously uttered the word. Furness thought that she might be thirsty, offered her a drink, and the animal accepted. But, who knows why? Almost pathetic was the way in which the docile little animal was trying her best to coöperate without apparantly grasping the point. After a time she offered to push the spatula against her tongue with her own hands. Here was something that master wanted, and she was eager to help. But what it was all about, or that she might utilize the lesson, quite likely never entered her consciousness. Furness quite properly concludes that the apes do not possess the faculty of language in the proper sense of the word.

Parallel are the results of Boutan, who worked with a gibbon, a particularly vocal species. The gibbon, he finds, is capable of no more than pseudo-language. Its sounds are like those of the other mammals in expressing emotions; they do not convey anything objective. Utterances relieve the utterer: there is no semblance of their being purposive as regards conveying information. The chimpanzee, in fact, does not confine himself to vocal utterances: when frightened he rattles a tin pan or thumps the wall of his cage. It is clear that we are beyond the realm of what can profitably be construed as language when we are driven to include the rattling of pans.

All in all, the data at hand are unanimous to the effect that the speech faculty of the apes is substantially on a par with that of a normal six-months old human infant: namely, nil. When we inquire why this is, it seems likely that however we may paraphrase it in more technical terms, the old reason literally holds: animals do not talk because they have nothing to say.

This fact is particularly striking because the structure of the mouth parts of the apes is so similar to that of man that there is no doubt that they could render reasonably close approximations to the sounds of human speech. They might talk with

a brogue, but we could understand them. What a parrot does when with his horny beak he produces effective imitation of a soft lip sound like "p," a primate could obviously do at least as well, so far as his anatomical apparatus is concerned. Yet he never tries to speak, nor apparently can he be induced to try, no matter how close his associations with humans.

HAVE APES A CULTURE?

There are three historic definitions of man designed to set him off functionally from the other animals: man is the speaking animal; man is a political animal; and man is the tool-using animal. Other phrasings, such as the fire-using or clothes-wearing animal, are evidently included under the more general category of tool-using. We have considered the first of these criteria, that of speech, and found it to hold. The second definition goes back to Aristotle. It has been said that, the connotations of words having changed, Aristotle, if he were living now and speaking in English, would make his definition run that man is a social animal.

We still know very little as to the kind of society the apes maintain in a state of nature. Their behavior in captivity, with dependance primarily on human beings instead of fellow apes, evidently is little indication. With a few exceptions, those observed in captivity have been immature. Natural history observations will obviously be extremely difficult. That the apes are sociable is evident but not to the point. Dogs, birds, some other species, are highly sociable toward human beings. Of course if man were not endowed with a gregarious impulse he could not have developed culture; but something more than gregariousness is needed to produce culture; otherwise cattle would possess it. Now it is conceivable that the chimpanzee and gorilla possess something more than sociability or personal attachments; that they pass down from individual to individual and from family to family certain forms or patterns of relation to one another—traditional group habits, which may have begun to take on something of the color of institutions. But that this actually has happened without the presence of speech is difficult to conceive; and there are no positive indications whatever as to the existence of such incipient institutions. It would not be difficult to project backward from the simpler human social institutions to something that seems still simpler and expectable among apes. But experience has shown that such reconstructions are always in part misleading, and quite likely to be unfounded. As regards the question, then, whether the apes are in any rudimentary degree social animals in the sense that man is institutional, we can at present answer with nothing more than a question mark.

It may be thought that there are some evidences warranting a less skeptical attitude. Koehler reports that when a pair of his young chimpanzees in playing began to stamp and circle about a post, others frequently ranged themselves in line until they formed a ring, and presented much the appearance of a savage tribe in a dance. But, while the stamping of each ape was definitely heavier with one foot, there was no unison—only a tendency to keep time together. And there was nothing to show that the dancing followed any pattern—that there was imitation in the cultural sense, with social acceptance of a form. The dancing of one individual stimulated other individuals into analogous behavior; but the performance of each apparently remained a purely physiological response. When the gamboling of one lamb sets others to gamboling, or when one startled sheep runs and the flock follows, the sheep do

not possess culture because they follow one another's example. If one ape devised or learnt a new dance step, or a particular posture, or an attitude toward the object about which the dance revolved; and if these new acts were taken up by other chimpanzees, and became more or less standardized; especially if they survived beyond the influence of the inventor, were taken up by other communities, or passed on to generations after him,—in that case we could legitimately feel that we were on solid ground of an ape culture. But of this there is as yet no indication.

It is the same with chimpanzee fashions in smearing white paint, or teasing chickens, which Koehler describes. These are comparable to the vogue which a game or social manner or dress fashion has among ourselves; to the fact that the first boy who brings out his kite or his marbles in spring is almost certain to set other boys of his school to bring out their kites and marbles. What is cultural in such phenomena is not the fact that one individual leads and others follow, but the game or fashion as such. The kite, the manner of manipulating the marbles, the cut of a garment, the tipping of the hat, remain as cultural facts after every physiological and psychological consideration of the individuals involved has been exhausted. Of any such institutional residuum of unmitigatedly cultural material, there is as yet no demonstration among the apes.

THE USE OF TOOLS BY THE APES

When it comes to our third criterion, that of tools, the case is different. The anthropoids use tools; and they make them. Chimpanzees take up sticks to draw to themselves food which is beyond reach of their arms. They beat with sticks for the same purpose, or cast ropes or ropelike objects. If the desired food is out of reach overhead, jumping to reach it has led to failure, and there is no other individual about that can be climbed onto and used as a take-off for a higher leap, many of them finally have recourse to moving a box or other convenient object under the prize. If, after they have learned to use a box, the food is hung still higher, they learn to pile a second box on the first; and the more versatile ones will pile three or four. Gorillas will also do this. As Koehler justly points out, the piling of the second box on the first is psychologically a quite different thing from moving the first box; there is in it the element of combination, or construction. The difference is like that between rolling a stone and building with stones.

If the convenient reaching tool happened to be a bundle of straws, one chimpanzee, finding the straw too soft to move a banana, without hesitation stiffened the bundle by doubling it. Even then the tool was ineffective, so she redoubled it. That it was now too short to reach the banana rendered the result ineffectual, but does not detract from her credit as an inventor: she got the problem and knew what to do about it.

Especially interesting is the observation that two canes were joined one into the other to draw in food which lay beyond the reach of a single cane. This is indubitable tool making; especially when a stick is chewed down to fit into the hollow of a cane.

How far chimpanzees under proper stimuli might progress in devising tools for themselves is difficult to say; just as the observations leave it somewhat obscure how far slower-witted individuals tend to profit by the discoveries of a more inventive one. There are however some interesting observations as to the circumstances of the process of invention.

First, the chimpanzee strongly dislikes the strain of situations which call upon his inventive faculties. The process of invention is visibly and disagreeably arduous for him. His first impulse is to give up, or to become angry, if he cannot arrive at a solution by purely physiological means such as leaping or biting. Characteristic is the fact that if a reaching implement is in line of vision with the desired object, it is usually promptly utilized. If on the other hand, the stick lies behind the ape's back as he faces the food, it will not be "thought of" or noticed and taken up for a long time, when the experiment is a novelty to the animal being observed; in fact, usually not until after repeated renunciations and recurrences of desire. Emotions clearly are important, constituting a strong resistive factor. The individuals that meet difficult problems most readily, and carry invention farthest, are evidently those best able to control or inhibit the emotions which the prospective goal arouses in them.

COMPETITION AS A STIMULUS TO INVENTION

But emotions of another kind can be an impelling influence toward invention. These are the social emotions. His desire for affection, and for approbation from human beings, certainly helps a chimpanzee to invent tools. In the state of nature it is probable that competitive emotion—jealousy—is even more stimulating. Significant is Koehler's observation of the behavior of his adult female chimpanzee when a loaded box or heavy obstacle was placed to prevent her from reaching her food beyond the bars. She was perfectly capable of moving the obstacle; but the problem weighed on her for two hours. When however one of the young animals began to stray in the direction of the food, from which it was not separated by bars, she suddenly seized the heavy box, shoved it out of the way without hesitation, and grasped the prize out of reach of the competitor. Next day she found the solution in one minute.

The same chimpanzee objected to using sticks for reaching unless they were, so to speak, thrust into her hands by their placement. For half an hour she neglected a stick which was close behind her and which, as a retinal image, she saw whenever in aimless irritation she turned around. After a while she stood on the stick. She must have felt it with her sole; but again, as a personality, she refused to receive the sense impression. After half an hour a free chimpanzee came near the food. The jealousy which his approach excited was utilized to repress the sulking emotion hitherto displayed; and suddenly the ignored stick was perceived, seized, and used to draw in the food.

The one gorilla tested reacted less emotionally, but showed less inventive faculty than the cleverest of the chimpanzees.

These observations may not throw much light on the question of how far apes possess culture. They do however suggest much as to the psychology which underlies human culture, and what we are accustomed to term its progress. They indicate that the elimination of the competitive factor among men would deprive civilization of one of its principal and perhaps indispensable impulses. They suggest further why the institutions, codes, and ethics of all peoples have so strongly emphasized inhibition; why, for instance, courage—the repression of fear—has always been esteemed a high if not the highest virtue; and why, similarly, all social groups condemn incest. Not that the anthropoid apes set up moral standards. But all human groups do; they have evidently learned, on the basis

of individual life experiences, the social importance of restraints. The inference would be that from soon after the time when men began to possess institutions, and were able to formulate these in speech, they have never seriously swerved from an insistence on a social limitation of the natural sex impulse.

PLAY AS AN ELEMENT IN INVENTION

Play is evidently an important element in chimpanzee invention. Situations are often first met, or devices prepared, not from a desire to achieve a useful end, but as a matter of sport or amusement, as a means of satisfying pure manipulative interest; the utilization is later. Here again we have parallels with human culture. The lodestone or magnet was long a toy, or an object of pre-scientific marveling, before it was used in the compass and still later in machinery. The Chinese placed a compass on "south pointing chariots," where it could have served no purpose other than as a refinement of luxury, nearly a thousand years before they employed it in the serious business of navigation. They knew gunpowder in fireworks centuries before they put it into firearms. In fact, in both cases the Chinese play invention seems to have passed to other peoples, the Arabs and Mongols, to have been turned by them to more practical purposes, and then to have been re-introduced into China.

The domestication of animals, although its whole history is far from clear, appears to derive at least in part from the keeping of pets. To be sure, the keeping of a pet, which may be played with so long as it is amusing, and allowed to starve or escape when it becomes troublesome to maintain, is a different thing from the tiring business of continuously caring for flocks on which living depends. Also, of the numerous species of animals which are interesting enough as pets, many are of no economic utility, and others are incapable of being domesticated to the point where they can be regularly handled and fed and reared with economic profit. Still, it is clear that many primitive peoples who never rear either domesticated animals or plants do keep pets frequently. It can hardly be doubted, therefore, that a stage of play domestication preceded economic domestication of animals in the course of human history.

Among us occidental moderns the process of invention is difficult to understand; perhaps because we cannot yet sufficiently extricate ourselves from our own civilization to look upon its processes with the same objectivity with which we view those of foreign or ancient cultures. Nevertheless, one thinks of the pneumatic tire, first employed on the bicycle in the period when this was a novelty and instrument of sport, but gradually helping the motor car to develop into the important element which it now forms in our economic structure.

SCIENCE AS A FORM OF PLAY

Modern invention is of course completely interwoven with modern science. Now, time and again scientists have pointed out, sometimes when they were asking for money and sometimes when they meant what they said, that the progress of applied science or invention depends on the progress of pure science or discovery. Researches which, at the time they were made, could not have been conceived of as leading to practical results, have nevertheless again and again led before long to the invention of useful contrivances. The whole history of electrical discovery is a case in point. Now the significance of this, in the present connection, is that pure science is, after all, play. We are accustomed to think of

it as hard work because it requires intense specialization and long application. But in these qualities it agrees with modern sport. Like modern sport, it is, economically and physiologically, immediately useless. It is even more than useless: it is unnatural—a fact often charged against organized sport, but just as true of science. There is in us an element making us strive for mastery or excellence or perfection of achievement for its own sake, apart from the satisfaction of any definable physiological need. It is the driving of this impulse to the point of physiological discomfort, even of bodily strain or damage, that gives sport and science their quality of unnaturalness. At their fullest, they are perversions of the play impulse.

No chimpanzee seems capable of being so perverse: he is too unintelligent, from our point of view; but also too sensible, too concordant physiologically. For better or for worse, however, we men are prone to this exaggeration of the play impulse; and, again for better or for worse, the exaggeration has perceptibly aided the gradual accretion of the stock of modern culture, as well as the betterment of athletic records.

The chimpanzee, in his youth, is as playful, restless, curious, and explorative as any human being. He does not go very far in tool invention, because his central nervous system seems to become quickly and healthily fatigued by play which puts on the nervous system any strain that cannot be promptly discharged into striped muscle activity. He is physiologically a clear extravert. The gorilla, on the other hand, is described as an introvert, with more self-respect and sense of value of his personality. It remains to be seen whether in the field of pure intellect the gorilla will prove the equal or superior of the chimpanzee, once we have learned to establish relations with him satisfactory to his temperament.

A demonstrated psycho-physiological trait of the ape is lack of patience in the solution of a problem. As soon as difficulties are encountered which cannot be solved by direct use of hands, feet, or mouth, the chimpanzee tends to take refuge in irritation or sulks; the gorilla becomes dignifiedly indifferent. An added stimulus, such as doubling the reward, or approach of a competitor, may launch him again at the task, and perhaps with success. But the effort is new, not continuous.

The fact is of interest because it finds a parallel in the history of culture. There was required actually less skill to fashion many of the ground or polished stone implements of the New Stone Age than some of the specialized chipped ones of the Old Stone Age, tens of thousands of years earlier. The average modern person who has never worked stone would, if the reward were sufficient, almost certainly turn out on the first attempt a better ground mortar or ground stone axe than a chipped knife or spear point, if indeed he would not fail utterly in the latter. The reason is that while chipping requires definite manual control, it is a very rapid process. A dozen failures occupy little time; each may suggest the possibility of an improvement; and the thirteenth attempt may be reasonably satisfactory. Grinding, however, although one of the simplest of operations, is of necessity slow. Early man was apparently readier to mobilize a fair degree of manipulative skill than a great amount of patience.

INVENTION BY ACCIDENT

That the chimpanzee possesses a beginning of ability to reverse his primary impulse is shown by a series of experiments by Koehler. After the animals had learned to use a stick to gather in food from beyond their reach, the fruit

was placed behind a barrier, in a low open box with only the farther side broken out. To get his banana the ape had therefore either to lift it with his stick out over the front or side edge of the box, which was difficult; or he had to reverse his first impulse of scraping the fruit toward himself, and instead push it farther away until it was clear of the box; after which of course the familiar raking-in process could successfully commence. Without exception the apes found this problem difficult. Some never solved it except when the box was partly turned to help them; others only by the aid of accident, such as the banana rolling favorably; and even those who had learned the necessary reversal, tended to relapse into their earlier, direct, impossible efforts. Still, some of them did learn, and with practise came to perform quickly and efficiently. These results are a genuine credit to the more gifted individuals of the chimpanzee species. More observations as simple and significant as this are a desideratum.

This experiment developed a type of success which probably has its parallel in culture: invention partly by accident. The banana, prodded by the stick, rolls or bounces near an open corner of the box, or entirely clear of it, and the animal immediately sees a solution that had been beyond its grasp while the problem remained unmitigated. After this partial aid by chance, the whole problem is soon mastered.

Whether invention wholly by accident occurs in human culture, may be doubted. But that accident sometimes assists, is likely. At any rate, there are devices like the bow and arrow, and the fire-drilling apparatus, which seem to be by-products of other devices subsequently improved or converted when a chance variation suggested a new utilization. A bow which fails to attain a certain efficiency is of no use as a weapon. Yet an efficient bow is a fairly complex implement of delicate adjustment with which a first inventor would be almost foredoomed to fail. Its origin is best conceivable as a secondary stage of a bow used as a toy or musical instrument, which, being later produced with the requisite strength and balance, would be serviceable for propulsion. We do know from archaeology that the bow came into culture relatively late—not until the terminal phase of the Palaeolithic. The fire-drill is a simple apparatus but needs to be adjusted and operated in a particular way before a spark is obtainable. Drills used for boring, however, would sooner or later be likely to produce smoke or even a spark, and a new application be suggested. It would be rash to contend that any invention was ever due wholly to lucky chance. If there were no insight into problem nor recognition of need, the accident would pass unobserved and unutilized. But it does seem that previous accomplishment, plus insight, plus accident, have at times led to the creation of new cultural material. And the same three factors occur in chimpanzee invention.

The chimpanzee depends much more than we on muscular strength and gymnastic skill. Even the most intelligent anthropoids manifest little sense of statics. They pile three or four boxes randomly and then balance their own bodies to counteract the imbalance of the mechanical pile. Boxes are set on an edge or corner and the animal tries to mount them—in some cases succeeds because of its natural acrobatic capacity. The one gorilla tested proceeded more like a human being in adjusting and trying out the boxes; but this was a proportionally heavy animal, and without jumping impulses. Of course a solution which

depends for its effectiveness on muscular skill is in that degree farther from an invention in the cultural sense. An imperfect tool suffices; the congenital body makes up the deficiency. If men had the strength of arm and jaw of the great apes, their enormous canine teeth, they would no doubt have continued for a long time to meet many situations with muscle rather than with tools.

The impulse to perform with his body is strong in the cleverest chimpanzee; performance with a tool is usually clumsy and always an arduous act at first. Given a suspended banana and an available pole, the first impulse is to climb the pole before it can fall and grasp at the fruit—a sort of pole-vaulting. Sticks are brandished threateningly in play combat. But let a chimpanzee lose his temper, and he drops his stick and plunges into attack with hands and teeth.

Nevertheless some use of tools is spontaneous. Stones are hurled. Sticks are used to dig in play or for roots, to tease fowls or other animals, to touch fire, lizards, live wires, or other things that provoke both curiosity and fear. In removing filth from his body, the chimpanzee prefers a stick, chip, leaf, or rag, to his fingers. He will lick up ants, or hold out a straw for the ants to crawl on and then lick them off. He has not been observed, outside of posed problems, to manufacture tools or to lay them aside for the future; he does certainly, without human stimulation, use simple tools that come to hand, and use them in a way that in a human being we should call intelligent.

INVENTION AS A SYNTHESIS OR AS A COMPOSITE

Sometimes an ape sits down in front of a problem that has baffled him, detaches himself from his previous efforts, and looks the situation over, seemingly thinking. How far he may actually study the situation is difficult to say; but he certainly appears reflective. Suddenly then, sometimes, the solution comes and is applied without hesitation or awkwardness. Again, it may come overnight and without warning. When a human being acts in this manner we say that he has thought the problem out. At any rate the ape's solution tends to come as a whole, as an abrupt synthesis.

Now as we think of the course of human culture, it may seem as if the layman conceived of invention happening by syntheses like those of the chimpanzee, whereas the social scientist tended increasingly to view its history as one of gradual accretion. Both are correct. What we call an invention is normally a composite of many inventions gradually assembled. Each unit invention, however, probably depends on one insight made as a synthesis—a simple one, mostly, but a synthesis. Popular imagination, with its love of the dramatic and abhorrence of the analytic, transfers the process operative in the unit to the ensemble. It makes the printing press, the steam engine, the telegraph, the radio, spring like Pallas Athena in full panoply from the head of some human Zeus. As an explanation of what happened, this is pure myth. The steam engine, the telegraph, the automobile, are obvious composites. They function as cultural units, but the process of development of each totality has been a complex and slow one. An automobile represents literally thousands of inventions. Its hundreds of parts, like the screw and the cogs, have each its history of successive stages, each of which was in its time an invention. As Gilfillan has recently shown, the reputed inventor of every machine is regularly that individual among a number of contemporaries who first made a given assemblage of existing inventions pay. In

the eyes of the world successful invention is successful economic exploitation. And however we may rebel ethically or aesthetically, this verdict has primary culture historical validity. It is when a machine makes money that it comes into cultural use and consciousness. At the same time, a scientific interpretation of culture must penetrate deeper and recognize the antecedent stages and gradualness of development; much as for reckoning our ages we count from the day of birth, but the biologist in studying life history goes back of that act of emergence into pre-natal life, to conception, and beyond that to the ancestral germplasm.

It is the innumerable minimal unit elements of human invention that find their rudimentary prototypes among the anthropoids in their qualities of discreteness and synthesis. Beyond that, the parallel does not go; for the interrelation and accumulation of these elements is a cultural process, and culture the apes as yet give no indication of possessing.

THE DESTRUCTIVE IMPULSE

Left to themselves, chimpanzees are destructive. They love to demolish. Like small children who have grown up uncontrolled, they derive immediate satisfaction from prying, ripping, biting, and deliberately smashing. Once they begin, they rarely desist until an object has been reduced to its components. They never learn to lace shoes; they find spontaneous pleasure in unlacing them. The impulse to construct is infinitely weaker; it is called into activity only by special problems, and the solution of these is trying. One of the few exceptions is nest building. This the chimpanzee does from an early age, and apparently without being taught. Here we seem to have a genuine case of what in the older terminology was called "specific instinct." Nest building is of interest because directed toward an objective outside the body. But, according to both Koehler and Yerkes, the building is partly a drawing and tucking of branches under the body. Some of the twigs snap off and tend to hold in place the branches which remain attached to the tree. In this way a tolerable mat or platform is built up. This however remains, during the act of building, in contact with the ape's body; it is built against his skin, he feels it during the process of construction, and the sensations aroused may be an important element in the carrying out of the process. Some chimpanzees, if trees were not available or loose material did not suffice, laid down a ring that outlined the body and merely suggested the nest—a nest gesture, as it were.

The powerful impulses of chimpanzees toward destructiveness may help to explain one phenomenon in the history of human culture already touched upon: the long precedence in time of the chipping over the grinding technique in stone. After all, the earlier and grosser process of production by fracture is one of breaking apart. Grinding, being so slow as to be almost imperceptible in its results, must be quite unsatisfactory as a means of satisfying the demolition impulse. As an object is slowly rubbed into form, there is probably rather a sense of shaping and constructing. Of course, the Chellean picks and other early Paleolithic artifacts are not mere by-products of an interest in cracking boulders; they are too definitely adaptive, too patternized, too utilizable as tools. But preceding the Palaeolithic there are the "eoliths" which have been championed by some and denied by others as the earliest tools. They date back to the Pliocene, if not the Miocene, much beyond the earliest fossils of organisms in the line of human descent. It is gener-

ally admitted that the eoliths were not fashioned as tools but produced by natural agencies and then utilized as tools. Their finer fractures, usually confined to one edge, are interpreted as the results of wear during such use, and not as deliberate attempts to produce an edge.

In the light of ape behavior we can venture one tentative step farther. Our ancestors, like chimpanzees and children and human adults, probably took pleasure in demolishing. Learning among other things to smash boulders, and especially nodules of flint which long resisted and then shattered cleanly, they may have found themselves provided with attractively sharp and shining flakes, affording a new toy. Manipulation of these may have led to the discovery that the flakes furnished the possibility of a new satisfaction in hacking or scraping other objects. From such play in turn might have grown increasing habits of tool use; leading finally, when the mechanism of culture fixation and transmission became sufficiently developed, to the manufacture of tools as tools.

THE ORIGIN OF CLOTHING

We have a few observations that bear on aesthetics and religion. The apes are indifferent about being clothed or dislike it, although they appreciate a blanket in which to wrap themselves at night. On the other hand, they voluntarily drape themselves with strings and rags, wearing these for hours or days. The satisfaction is clearly in the wearing as distinct from the act of putting on. As Koehler aptly says, the heightening of bodily consciousness appears to be what gives the pleasure. Chains or strings which swish and sway with the motion of the body are favored; a girdle would probably be meaningless, or its presence be resented. The suggestion is that human dress for protection and human adornment spring from separate sources. This has long been good anthropological doctrine. However, in the history of man, protective clothing and adornment intergrade so extensively that a large class of phenomena can only be described as ornamental dress. Even basically utilitarian clothing is invariably affected by the fashion impulse in man. One may conjecture that there have been two developments little related in origin which secondarily came to overlap; and that dress and adornment, as we know them in the history of human culture, are largely hybrid.

RUDIMENTS OF AESTHETICS

Koehler's chimpanzees, in digging, discovered some white earth. Tasting it and finding it inedible, they spat it out. Wiping their lips, they saw the wall whitened. This soon became a game. First with their lips and then with their hands they painted with white earth whatever walls and surfaces were available; but rarely their own bodies. There was no attempt at design or figure. The stuff was smeared on, and the more the appearance of a surface changed, the greater the satisfaction. The pleasure apparently lay in using the muscles to produce a visibly effective external accomplishment. The act of creation gave satisfaction.

These observations accord with the behavior of small children, whose first attempts at what we are wont to call drawing or painting, even when an attempt is made to guide them, normally result in nothing more than smearing. It is rather evident that the small child, left to himself, does not attempt to draw a house or a dog or a man. He converts a white paper into a red or black one, a monotonous into a variegated surface. He defaces as much as he makes. It is

again demolition pleasure; or, more generically, the satisfaction of producing an effect; and this, at an early stage of development, is more readily accomplished by destruction than by construction. We tend unjustly to read the child as an adult. It is doubtful whether small children ever try to represent except as the result of cultural influence. In fact, we do not know that a human being become adult without impingement of cultural influences would try to represent anything. So too, when a child makes something like a decorative pattern, his principal satisfaction perhaps lies at first in the rhythmic motion. We, thinking primarily of the effect, are likely to construe into the child an impulse to decorative rhythm and regularity, which it probably does not appreciate until later in life. To understand art, it seems necessary to recognize that there is always a motor impulse involved; that in incipient stages the motor element probably predominates; and that recognition of aesthetic qualities as such is, historically, likely to be an overlay.

ANTICIPATIONS OF RELIGION

Religion is difficult to conceive without formulated ideas and thus without speech. Even its rudiments could therefore hardly be looked for among the apes. Yet there may be some sub-cultural anticipations. Koehler made a rude rag animal with shoe-button eyes which vaguely suggested a miniature donkey. It was altogether too crude to be mistaken for a live animal, yet had sufficient resemblance to one to set it off from ordinary inanimate natural objects, or from artifacts such as boxes or chairs. The apes responded instantly with manifestations of fear. It was not terror as great as an ox or a camel inspired, but can perhaps best be characterized as similar in its expression to what human beings would call awe. There was not a trace of either the indifference or the curiosity which a lifeless object provoked; interest there was, but also respectful staying at a distance for a long time. Even food placed in proximity to the image was shunned, and only at last cautiously snatched with a precipitate retreat ensuing. Koehler observed a dog manifest the same degree of interest in the figure, except that, being a carnivorous and therefore aggressive organism, his interest took the form of hostility. He convinced himself however, as soon as he dared, of the inanimateness of the image; and from then on was completely indifferent to it. The chimpanzee, like ourselves, is less practical, evidently as the result of possessing more imagination. Occasionally however, one of the lower animals will react more like a man or an ape. I have seen a young dog for weeks manifest panic whenever an imitation animal toy was brought into his presence.

The relation to religion of the chimpanzee's reaction lies in his manifesting something like the awe which is regarded as an important or essential ingredient of what we call the religious feeling: the religious thrill. It is generally recognized that religion could not well originate without the presence of emotions of which awe may be taken as the type; and that these emotions tend to persist, or to be re-awakened in religion, no matter how culturally crystallized this becomes. Also, the kind of object that arouses the awe-like feeling in chimpanzees has a certain quality of resemblance to the basic concepts of religion. Souls, ghosts, spirits, like stuffed rag donkeys, do not occur in ordinary experience; like them, also, they are thought to be at once similar to living bodies and different from them. A dummy donkey with button eyes evidently is literally supernatural to

a chimpanzee. We can then say pretty positively that the ape does not have a religion; we can also say pretty positively that he acts at times as if he were religious.

When we put together the observations and interpretations just reviewed, it becomes clear that we have in the anthropoid apes beings remarkably close to ourselves. They are animals behaving in innumerable respects like men and differently from all other animals. Faculties which we are accustomed to regard as specifically human prove again and again to be present in them in rudimentary form. What they do lack totally, so far as we can yet judge, is speech and culture. In this regard they are as sub-human as the other mammals and the birds. This is really remarkable in view of their possessing some of the ingredients universally accepted as going into the makeup of culture: especially inventiveness. The ape will not only use tools, he will not only make them when he is taught, he will invent them. That the tools are simple and crude is expectable; that he can and does devise them makes us wonder why he did not pass on to develop an elementary culture. The absence of speech undoubtedly is an important factor in this deficiency. This lack of language faculty has been ascribed to a lack of imitativeness as regards sounds. This lack may be granted; yet one cannot help but feel that it is not a wholly sufficient explanation. Similarly, it seems doubtful whether lack of speech alone is sufficient to account for the total absence of culture. It may well be so; but it will require further experiment, or at least much more extensive observation, before we may be sure that there exist no other potent factors of deficiency.

IS INVENTION THE CHIEF FACTOR IN CULTURE?

With the ape inventive but cultureless, the question arises whether we have not perhaps hitherto exaggerated the importance of invention in human culture. We are wont to think of it as the creative or productive element in civilization. We tend to view the other processes in culture as essentially those of transmission, preservation, or decay. The idea of progress, which has so powerful a hold on the unconscious as well as the conscious thought of our day, may have led us to overemphasize the rôle of invention. Perhaps the thing which essentially makes culture is precisely those transmissive and preservative elements, those relational or binding factors, which social scientists have indeed occupied themselves with, but have been inclined to regard as after all of secondary importance in comparison with the dynamic phenomenon of invention. It may be that invention will prove to be what is incidental in culture; that it is merely a fashion of our day to look upon it as primary. What may ultimately be recognized as counting for more is the way the patternings of culture shape themselves to permit or prevent or induce invention, or, for that matter, any change of civilization. This shaping of patterns is in another aspect a matter of interrelations of culture material; and what appears to be indispensable for such interrelations to exist is a certain social relation, an organization, or form, or almost a standardization. The fundamental thing about culture then would be the way in which men relate themselves to one another by relating themselves to their culture material. This is perhaps not so far from the basic concept which Durkheim was trying to formulate when he succeeded in expressing himself in a manner that seems somewhat mystic. It must be admitted that the present formulation too is lacking in precision. But it is difficult to see with clarity into the murky area that lies on the edge of or beyond what we actually

know, in the region where we apprehend rather than understand.

If however the relational forces in culture phenomena are the intrinsic ones, then the indispensability of speech to the very existence of culture becomes understandable. It is the communications, perhaps, more than the thing communicated, that count. At any rate the fact that speech, to the best of our knowledge, is as thoroughly wanting among the anthropoids as is culture, tends to confirm this conception.

CONCLUSION

There is a residuum of new understanding which knowledge of the apes contributes to knowledge of human culture. We see above all the tremendous influence of the play impulse. We see the unit elements of invention sometimes made with the aid of favorable accident; more often occurring as a product of reflection, of a kind of synthesis which in ourselves we call ideation. We see, perhaps a little more clearly than before, the relation of these unit elements of invention to the course of invention; and how culture, in its operations, fixes and settles upon certain patternized combinations of these elements. It is these combinations, as combinations, which it allows to enter into its consciousness and deals with. We see also that the impulse of destructiveness has probably played at times an ultimately constructive part in culture development. We are able to recognize more clearly the rôle of the emotions with reference to culture, and of it toward them. Inhibition of direct and primary emotional impulses is a necessity for culture to acquire material with which it can build; and the existence of inhibitions has been felt by all cultures as indispensable to the preservation of themselves and of societies. On the other hand, emotion is also a positive factor. Competitive feelings in particular seem culturally stimulative; and we gather at least an inkling of the part played in religion by awe.

Many or all of these conclusions have at one time or another been reached tentatively or positively by anthropologists from the examination of human culture itself. The study of the anthropoids, however, yields grateful and valuable corroboration. Cultureless these higher primates are; but with reactions and faculties closely akin to our own, and manifesting at least some measure of the basal psychic ingredients which enter into culture. There is infinitely more to be learned from them by wise experiment, and no less by critical observation. We have only begun. In fact, with the wide interest in these animals, it is surprising how scant the significant scientific data on them as yet are. Further study of them is important in itself; it will be invaluable in the illumination of the basic problems of anthropology and all the social sciences; and will in turn be furthered by what it can derive from these sciences.

LIST OF LITERATURE

Yerkes and Child, in a late number of this Journal (2, pp. 37–57, 1927), have reviewed recent contributions to knowledge of anthropoid behavior and given a bibliography which makes a formal list of literature unnecessary. References here are by their numbers. The work of basic importance in the present connection is Koehler, The Mentality of Apes (47), a translation of the original (41) and (45). In (43) Koehler discusses some of the culture anticipations here considered. He seems to share my view that the anthropoids cannot be credited with culture. Very valuable are Yerkes' contributions (78), (79), (80), (81), plus two subsequent papers, The Mind of a Gorilla (Pt. 1 and Pt. 2, Genetic Psychology Monographs, Clark University, 2, nos. 1–2, 6, 1927). The latter of these two came to my knowledge after the present

essay was written and has not been used. Kohts's studies (48), (49), have not been accessible to me except through Yerkes' abstracts. They are rare in this country, are in Russian except for a German summary of (49), and evidently deserve to be translated in full. On the subject of language, Boutan (13), Furness (29), and Yerkes and Learned (81) are conclusive. Learned's portion of the latter is an objective record of chimpanzee utterances, probably accurate as to pitch but inadequate in other phonetic aspects. It is to be hoped that a phonetician can be interested in the subject. Similarly, on strength, Bauman (10), (11) has opened a subject which should be followed farther. Boutan's work (14), on mechanical problem solving by human children, brings in also anthropoid observations, and is marked by acuity and clarity of conception. Brehm's Tierleben in its last edition, edited by Neumann, (16), (17), reviews or quotes many of the older accounts, which are often extremely illuminating. As regards Garner, I concur with Yerkes: he knew his primates but misunderstood them.

ROOT HAIRS AND GROWTH

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WHY STUDY ROOT HAIRS?

GROWTH is the most complex of all biological processes. It is, indeed, a resultant of all of the physiological processes: absorption, synthesis, assimilation, conduction, digestion, respiration, and secretion. Any circumstance which affects any one of these physiological processes is likely to affect the rate or the type of growth. Thus the increased absorption of a substance may increase the rate of growth; or, on the other hand, it may retard growth, according to the kind of substance and the state of the organism. In general if the processes that tend to build up the organism, such as synthesis and assimilation, occur more rapidly than the processes which tend to tear it down, such as digestion and respiration, growth will occur. Growth may therefore be looked upon as the net result of physiological activity. It is a sort of index of the well being of the organism as a whole.

Growth however is not to be looked upon as the sum of all of the physiological processes. They are to be regarded more or less as aspects of the activity of the organism as a whole. Growth on the other hand is fundamentally a cellular phenomenon. While its rate is determined by the resultant of the physiological processes, it is itself a combination of cytological processes. It embraces, in fact, three phases of cell activity: division, enlargement, and differentiation. Cells undergo development in three ways. They divide, they enlarge and they differentiate. By differentiation is meant the change of an embryonic cell into a tissue cell. This change may consist in an alteration of form, composition, or content. It may mean the appearance of new organs, such as plastids, vacuoles, and so forth. It may, on the other hand, mean the disappearance of the nucleus, as in certain of the blood corpuscles or in sieve tubes; or the entire protoplasm of the cell may die and decompose, leaving only the thickened cell wall, as in certain of the plant fibers or conductive vessels.

We may, it is true, determine the growth of an organism by determining its increase in size or weight. Especially in the case of plants the increase in size or weight of only a portion of the organism, as the fruit or tops, may be taken; or it may be only of a portion of the constituents, such as dry matter or ash. By obtaining such data we can ascertain the effect of certain external conditions upon the state of the organism as a whole, without analyzing its effect, as to whether it stimulates or retards absorption or assimilation, etc., or as to how it affects cell division or enlargement or differentiation.

It is apparent that while such studies are useful in increasing our knowledge of the effect of external conditions upon crop production and such practical considerations, they cannot go far in extending our

understanding of the fundamental nature of growth. In order to understand the physiology of the plant or animal it is necessary to place it under as nearly constant conditions as possible, and then to vary one condition and measure the effect of this change upon one process as nearly as possible. In like manner, in order to study the growth of an organism intimately, it is desirable to proceed in the same way, noting the effect of the change of one external condition upon one of the cytological processes of cell division, cell enlargement, and cell differentiation.

The past fifty years have witnessed a very intensive study of the mechanism of cell division, beginning with the work of Strasburger and Flemming. The study of nuclear division has been especially thoroughly prosecuted, largely because of the connection which has been established between it and the study of the transmission of hereditary characters. But we are still a long way from understanding how hereditary factors bring about the characters of the organism during its individual development, largely because we have neglected the study of the other phases of growth. We have not as yet determined how it is that conditions determine the plane of partition or the rate of cell division, cell enlargement, or cell differentiation. In order to do this it is desirable that cells be chosen which undergo essentially only one of these three processes to the almost entire exclusion of the others, and which can be studied while growing normally under constant and controlled conditions.

In the study of cell division this ideal can be almost realized by the use of bacteria and other microörganisms in which there is little differentiation or cell enlargement, and in which the rate of cell division can be measured by counting the number of cells from time to time. But there is such a wide gap between the cell of the microorganisms and that of the higher plant or animal that it is doubtful whether we are at all justified in applying the conclusions from the one to the interpretation of the other. The nearest approach to a satisfactory study of the effect of conditions upon the rate of cell division in higher organisms is by the method of tissue culture. This is, however, open to the criticism that the cells doubtless behave entirely differently in these cultures, than they do in their normal relation in the organism.

A much more satisfactory study can be made of the effect of external conditions upon cell enlargement through a study of root hairs. These are projections of superficial cells of the roots of plants. They are normally cylindrical in form, and enlarge only by elongating. A measurement of increase in length gives us a means of directly calculating the increase in volume of the cell, and hence its enlargement. The root hairs are produced, even, upon very young seedlings. This makes it possible to study root hair elongation while the entire plant at that stage is intact. The root can be allowed to extend into a moist chamber, or into a vessel of solution on the stage of the horizontal microscope. In this way we can have the plant under normal and controlled conditions and measure accurately its response to different factors of the environment in terms of cell enlargement, withoutcomplicatingcircumstances. The nucleus of the root hair does not divide, neither is there any other evidence of cell division occurring within the cell. The process of cell differentiation is reduced very nearly to a minimum. It here consists of an extension of the cell wall and an enlargement of the vacuoles incident to cell enlargement. There is probably a slight change in the composition of the

cell wall, but there is normally no thickening of the wall, nor any apparent differentiation of structure or substance within the root hair during its elongation.

Not only are root hairs desirable objects for use in the study of cell enlargement, but they also afford one of the most accurate means of ascertaining the biological effect of various physical and chemical agents. They can be readily exposed to different types of light and other radiations. Experiments can be arranged so that temperature can be accurately controlled and its effects investigated upon a cellular basis. Root hairs can likewise be subjected to various types of electrical phenomena.

It is, however, in the realm of chemical agents that they lend themselves to the greatest diversity of experimentation. The chemical substances which may be presented to roots of plants may be classified into four groups according to their effect upon the plant. They are either nutritive, that is, actually utilized in the construction of necessary organs and compounds; or they are toxic, that is, they have an injurious effect upon the rate of plant processes or cause abnormal development; or they are stimulating, that is, they accelerate plant processes above the normal; or they are neutral, that is, have none of these effects.

Root hairs are especially well adapted for the study of the biological effect of chemical elements and compounds, in that they grow either in air, so that gases may be studied, or in solutions, so that inorganic and organic soluble compounds may be used. The only element that is necessary in addition to those in water is calcium. Therefore they can be grown in so simple a solution as calcium hydroxide. Other soluble substances can be studied by adding them to calcium hydroxide, and hence having them in a very simple solution. In this way the various nutritive, toxic, and stimulating agents can be thoroughly studied as to their biological effect in various concentrations and under various conditions of light and temperature and of degrees of acidity and alkalinity of the medium.

In studying these chemical factors it is obviously advisable to investigate the nutrient constituents first. Only after they are completely understood can we hope to make a careful analysis of the stimulating and toxic substances. We know that certain elements, namely, nitrogen, potassium, phosphorus, magnesium, iron, sulphur, and calcium are actually utilized in the construction of plant tissues. These are certainly to be regarded as nutrient elements. Certain others, such as sodium, chlorine, manganese, and boron seem to be present in most plants, and may eventually prove to be of direct nutritive value.

The study of the nutrient constituents of plants began with the chemical analysis of wild plants and of the soil upon which they grow. As the science of chemistry has developed this study has become more and more intensive and extensive. The study of cultivated crops and fields was undertaken in the same way with more dependable results because of the more uniform conditions. If such investigations were made in experimental plots especially planned for this purpose still more consistent data were obtained. A further improvement consisted in growing the plants in greenhouses in benches, flats, or pots, where temperature and humidity could be somewhat controlled. But even here the complexity and variability of the soil made definite conclusions very difficult. A very important advance was then made by growing the plants in sand to which nutrient elements were added in the form of simple inor-

ganic salts. Still better results were obtained by using solutions in jars, so that the roots were not in contact with any solid substratum at all. In this case it is necessary to supply the roots with oxygen by bubbling air through the culture solution from time to time. It was also found that the composition of the solution changes rapidly owing to the absorption of some substances from it more rapidly than others, and the liberating of substances, especially carbon dioxide from the root. This difficulty may be overcome by an elaborate system of growing the plants in a flowing solution.

But even this most refined method of studying the balanced rations of plants has not given as conclusive results as are desired. One of the difficulties consists in the long period of time required to raise the plants to maturity, even in these solution cultures. So many things may occur during the course of several weeks which may have an effect upon the final results, that it becomes somewhat uncertain just what to attribute to the effect of the one element which is being studied. In order to raise plants to maturity there must be present in the solution at least seven mineral elements. This means at least three or four salts. To discover the specific effect of each of these elements then becomes a problem, because of the interactions which are known to occur between them. Finally there is the difficulty of finding an exact criterion of the degree of development of an organism such as one of the higher plants. As noted above increase in size, weight, dry weight, etc. are the resultant of so many processes, and are in addition affected by so many external conditions, such as disease, insect activity, light, etc. that their value as a a basis for judging the well-being of the plant is seriously impaired.

There is need then for a new method of investigating the effect of the respective nutrient elements as well as the toxic and stimulating factors in the environment of a plant. It seems that a study of cell enlargement of root hairs affords a logical opportunity to do this, inasmuch as they are in part, at least, the absorptive organs of the plant. As noted above, the history of the study of the balanced rations for plants represents a series of progressive simplifications of conditions surrounding the experiment. First plants were studied as they occur in nature. Then they were placed as nearly as possible under the same conditions as far as soil was concerned. Next wind and many animals were shut out, and the temperature and humidity of the air were held more constant. The next step was to exclude the organic matter of the soil; and following that the entire solid matter of the soil. Finally the gaseous and mineral content of the medium was controlled and kept rather constant. It is now desirable to simplify the experiment still farther by confining the study to just one of the phases of growth, such as cell enlargement, studying as far as possible each of the nutrient elements individually, before putting them together to form a balanced solution. Furthermore there is the desirability of studying the plant during a shorter period of time, during which light will be unnecessary, and the temperature, and acidity or alkalinity of the medium can be kept more constant. The study of the rate of growth of root hairs affords this opportunity.

We can determine first the rate of elongation of root hairs in different concentrations of calcium hydroxide. Inasmuch as this is a basic compound, increasing the concentration means also increasing the alkalinity of the solution, so that, when we have studied different concentrations of calcium hydroxide we have also studied

different degrees of alkalinity. We can next use a neutral solution of calcium nitrate of different concentrations. This contains calcium ions (Ca) and nitrate ions (NO_3). By adding calcium hydroxide to calcium nitrate we can study the effects of different degrees of alkalinity for different concentrations of calcium nitrate. In this way we can obtain a rather exact idea of the specific effect of the nitrate ion (NO_3) and of the hydroxyl ion (OH). By adding nitric acid, HNO_3, to calcium nitrate, we can study the effects of different degrees of acidity for different concentrations of the calcium nitrate, and in this way obtain information regarding the effect of the hydrogen ion (H). This same method can be repeated with calcium sulphate, $CaSO_4$, and calcium phosphate, Ca_3PO_4, thus obtaining a knowledge of the effect of the three nutrient anions, nitrogen, sulphur, and phosphorus, and also of one cation, calcium. The other three most important nutrient elements, potassium, magnesium, and iron, are cations. It is therefore necessary that they be studied by mixing their salts with those of calcium, inasmuch as calcium is necessary in order for root hair elongation to occur. We shall therefore have to study a solution of calcium nitrate, $CaNO_3$, and potassium nitrate, KNO_3, in different proportions, different concentrations, and different degrees of acidity and alkalinity. In the same way we can study magnesium nitrate, $MgNO_3$, and ferric nitrate, $Fe(NO_3)_3$. By studying the sulphates and the phosphates of these compounds in the same fashion, and then combining them in different ways, we can gradually build up the balanced culture solution with a thorough knowledge of the specific and mutual effects of each of its constituent parts.

It is therefore important that a study of root hairs be conducted intensively and extensively, in order to increase our knowledge of the nature of cell enlargement as bearing on the general problem of development, and from the standpoint of our knowledge of the biological effects of the respective nutrient, toxic, and stimulating features of the environment of the plant, especially of its roots.

THE FUNCTION OF ROOT HAIRS

Root hairs do not ordinarily occur over the entire surface of the root. The terminal portion of the root, consisting of the root cap and the regions of cell division and cell enlargement, does not bear hairs. Also the older portion of the root, that is, the part nearest the stem, is usually devoid of hairs. In fact in most roots the hairs are confined to a region between one and four centimeters in length near the tip of the main root and of the secondary roots and their branches. The hairless tip is usually of somewhat less extent; and, aside from the root cap, a protective structure which covers the tip, it is a region of growth, giving rise by cell division and cell enlargement to the region of root hairs above. By virtue of this elongation of the cells in the upper part of this region of growth, the tip of the root bearing the cap is pushed farther and farther into the soil. The region of root hairs is for the most part a region of cell differentiation. In it the surface cells produce protuberances which become the root hairs. The interior cells, on the other hand, become differentiated into the various cells of the older portion of the root, such as conductive cells, storage cells, etc. It is thus in this region of root hairs that the conductive tubes of the root, which are continuous with those in the stem, terminate as we follow them down the root, or originate as we trace them toward the stem. By virtue of the fact that the region of root hairs is being

added to by the region of growth below and in turn is giving rise to the older portion of the root above, it is a region which is migrating progressively farther and farther into the soil. Continually the root is adding new cells which give rise to root hairs in the lower portion of this region, while the older root hairs in the upper portion are collapsing and being sloughed off. The region thus presents a series of root hairs, gradated according to length, with the shortest near the distal end and the longest at the proximal end. The root hairs are thus usually short-lived structures, being formed by continuous elongation for a few hours, and then, after growth ceases, in most cases collapsing and being sloughed off in a few days.

There are, however, some exceptions to these rules. Cowles reports (7) that the prickly pear cactus, *Opuntia*, has root hairs to the extreme root tip. McDougal (52) has found them persisting over 15 or more centimeters of the root length of certain woody legumes, as the honey locust, red bud, and Kentucky coffee tree, for a period of several months. It is likely, however, that these hairs persist upon the root for some time after they die. He reports that in all except the younger stages they are thick-walled and brown in color and about four times their typical diameter. These root hairs, then, unlike those of most plants, undergo some cell differentiation, as well as elongation. McDougal correlates the persistence of root hairs in these plants with absence of root nodules. Miss Whitaker (86), however, found persistent root hairs in other groups than the legumes. She correlates this habit with a suppression of growth of the root in diameter. In a number of the Compositae, as asters, golden rods, dahlias, chrysanthemums, etc., she found them persisting even for two or three years.

The function of root hairs has been the subject of discussion ever since they were first figured and described in the latter part of the seventeenth century by Malpighi (50) and Grew (28). These two botanists, the one an Italian and the other an Englishman, laid the foundations for plant anatomy. They both found the root hairs and studied them in a general way; but they differed in their opinions regarding their function. Malphigi thought that they were the organs of absorption of the plant; while Grew considered that the plant absorbs through its tip, especially through the root cap. From this time on, for a century and a half, botanists differed upon this point. Their evidence regarding it was conflicting, owing probably to using different kinds of plants and to inexact methods of experimentation.

In 1837, however, Ohlert (57b) performed experiments which seemed to be conclusive. He used peas, lupines, and marigolds, cutting off the hairless root tip and covering the wound with lacquer. He found that the plant grew normally, showing that the root absorbs through the lateral surfaces upon which the root hairs were disposed. Meyen (56) in the next year concluded that the root hairs were the organs of absorption of the plant. He pointed out that they increase the surface of the root and extend the area of absorption. This conclusion has been accepted almost without question by the leading botanists to the present day. Persecke (62) thought that they were able to condense water from saturated air and absorb it. Mer (54) in 1880, however, showed that they must be in contact with liquid water in order to absorb it.

In 1883, Schwarz (73), who made the first extensive study of root hairs, considered their function more intimately. He calculated that they increase the surface of the root from 5.5 to 18.7 times

according to the species studied. It would therefore seem that by increasing the surface of the root they increase enormously its ability to absorb. However, this deduction of Schwarz should not be taken without more careful consideration, as it is very easily misconstrued. It is likely, in fact, that they do not increase the capacity of the root to absorb water at all. All of the water absorbed must enter the root proper through the base of the root hair, and since the walls of the surface of the root are apparently perfectly permeable to water, no more can pass into the root proper through the base of one of these hairs than could enter through the same area if no root hair were present there at all. That is, a root immersed in water can probably absorb no more water by virtue of its root hairs than it could absorb if it had no root hairs at all. The advantage of the root hairs in the absorption of water is, however, that in the usual situation in the soil, they extend out and come into contact with supplies of water which would not otherwise come into contact with the root at all. They therefore increase its ability to obtain water from a more or less dry soil, though they do not, apparently, increase its total capacity to absorb water.

With regard to salts, the root hairs doubtless have the same advantage of extending to new supplies of the salt not otherwise accessible; but they also probably actually increase the amount of salt absorbed due to the increased surface. This is due in part to the fact that the cells are not perfectly permeable to the salt, and hence more can enter the root through the base of the hair than could enter through that area devoid of a hair. There is also the effect of protoplasmic streaming to be considered in connection with salt absorption. As will be shown below the protoplasm in most, if not all, root hairs is in a state of circulation to and from the cell proper. This means that once a molecule of salt enters the cell it is likely to be quickly carried into the cell proper, thus giving opportunity perhaps for additional absorption of the same salt by the root hair.

However there have been a few studies from time to time which seem to raise a question as to the absorptive function of root hairs. Mer (53) raised the question in 1879, but presented no definite evidence bearing on the point. Frank (26) in 1887 determined the location of absorbed KNO_3 by staining roots in diphenylamin-H_2SO_4 after they had been growing in a solution of the nitrate. He found it in the region of elongation upon which no root hairs had been developed. Kny (40) repeated the experiments in 1898 and obtained the same results for aqueous media, but he points out that in the soil the reaction occurred in the region of root hairs since they extend nearer to the tip in the form used. Overton in 1902 found that root hairs of *Hydrocharis* are plasmolyzed in most, if not all, inorganic salt solutions and hence he concluded that they do not absorb. Coupin (6) in 1919 found that roots grew about twice as fast when only the tip was immersed as when the entire root was under water. But he does not preclude the absorption of water condensed on the root hair in the saturated atmosphere above the water in the first case, nor does he demonstrate that there was an adequate oxygen supply for the entirely immersed roots. In a later paper he contends definitely that not only does the root tip absorb, but also that the root hairs do not absorb. However, he does not present evidence which is convincing in this regard. Turina (80) worked with salts which he found were absorbed from the solution and deposited in the root cap

and in the region of cell division. This has been taken as evidence that they entered directly at this point. Priestly and Tupper Carey, on the other hand, have studied the chemical composition of the cell wall in the root tip and find that it contains proteins and fats or fatty acids. These they regard as the substances which render these cells impermeable, or at least, not freely permeable to water. Dissolved substances may, however, enter these cells and hence they are able to divide, whereupon they may take up water and become cells of the region of elongation.

Recently Popesco (64) has presented an extensive study in which he attempts to discover just which region of the root does absorb. His method consists in placing the roots in solutions of dyes, such as eosin, neutral red, and methylene blue and noting the parts which become stained. He also covered different parts of the root with cacao butter and noted the rate of absorption of water and of dyes. Finally he impregnated the root with potassium nitrate or iron sulphate by allowing it to grow in a solution of one or the other of these compounds and then sectioned and stained it so as to detect where the nitrate or sulphate was located. He concludes that plants absorb water from a solution just as rapidly if they have no root hairs as if they are well supplied with them. He finds that the root does not absorb through the root cap, but that the region of absorption bears a definite relation to the internal structure of the root. That is, it is located in the vicinity of the lower ends of the conducting tubes, rather than being defined by the location of the superficial root hairs. It usually happens, however, that these two regions are somewhat the same, that is, the tubes usually end in the vicinity of the region of the young root hairs.

From his work it would seem established that the surface of the root in the region of root hairs and immediately below it, that is, in the region of cell elongation, is as readily permeable as are the root hairs. However, it does not seem that he has demonstrated that root hairs are not absorptive organs. In the first place it must be borne in mind that much of his work is based upon the penetration of dyes and not of water. In the second place his study shows upon his own criteria that in many cases, the younger root hairs especially do absorb. Furthermore from the results of experiments to be described below, it is doubtful whether he has given proper attention to the effect of immersion in a solution upon the growth of root hairs already formed, frequently causing a cessation of elongation, and to the production of new hairs after immersion.

That root hairs actually do absorb salts is shown by the interesting experiments of Osterhout (59). He found that when root hairs are immersed in a calcium solution and observed with a microscope equipped with a Nicol prism, crystals are seen to form in the root hairs. These crystals he identified as being of calcium oxalate. It is thus apparent that the calcium ions have entered the cell and combined with the oxalate ions present there in solution in the form of oxalic acid or potassium oxalate or some other salt, and that there has resulted a precipitation of the insoluble calcium oxalate in the form of crystals.

This point is borne out by the common observation that when seedlings are transplanted from a hot bed to the field, for instance, it is necessary that they be shielded from sun and wind for perhaps 24 to 36 hours in order to avoid wilting and possibly the death of the seedling. Inasmuch as about this length of time is required for the root to develop a new com-

plement of root hairs, it seems reasonable to conclude that under normal conditions the root hairs are of immense importance in supplying the plant with water.

Schwarz (73) also pointed out that root hairs have another function in addition to absorption, namely, anchorage. They secrete material which dissolves the surface of solid bodies in the soil, forming a cement which fastens them firmly to these soil particles. In fact, if a plant is pulled from the soil, the root hairs will either bring the soil particles to which they are attached along with them, or they will separate from the root, but not from the soil particles. It therefore appears obvious that they have a function in anchoring the young seedlings. They could have no such function in anchoring the older plant, inasmuch as branching of the root system and root contraction performs this so much more effectively. In the young seedling this function of anchorage of the root hairs is very important. It is not so much that it prevents the plant from being pulled out of the ground. Such a circumstance is a relatively uncommon experience. It does however prevent the soil from being completely washed away from the seedling in case of watering or of hard rains. But it has a still more important relation than this. It prevents the seedling from pushing itself out of the ground. The region of cell elongation is just below the region of root hairs. It is that region in which the cells elongate parallel to the axis of the root, and push the root tip into the soil. In pushing the tip into the soil, the latter obviously encounters resistance. The exertion of a considerable pressure is therefore necessary. Were it not for the root hairs which bind the region above to the soil, the exertion of this pressure of elongation would result in the upper part of the root being pushed up out of the soil, instead of the lower portion being pushed down into it. This is then the most important, because it is the most frequent anchoring function of the root hairs.

Hill (34) has pointed out an additional function of the root hair, namely that it is able to adjust the absorbing surface of the root to the concentration of the soil solution. The latter is likely to become greater as a result of evaporation of water from the soil, or to become weaker owing to rains or leaching. It is therefore desirable that the absorptive cells be newly formed from day to day to cope properly with these changing conditions. The progressive elongation of the individual root hairs, the progressive formation of new root hairs, and the migration of the root hair zone, accomplish this adjustment in an admirable manner.

STRUCTURE AND COMPOSITION OF ROOT HAIRS

Meyen (56) in 1838 was the first to give an accurate description of the structure and development of root hairs. According to Schwarz (73) they vary in maximum length in land plants from 0.24 mm. in *Vicia* to 3.25 mm. in *Tradescantia*. In aquatic plants they may attain a length of 5 mm., as in *Potomageton*, and of 8 mm., as in *Trianea*.

It is thus seen that a teleological explanation of their existence will hardly do; that is, we cannot say that a plant has root hairs because it needs them in order to absorb or to anchor the plant, inasmuch as the plants having the longest root hairs are those which need them neither for anchorage nor for absorption. On the other hand it is to be noted that the duckweed, *Lemna*, a free floating aquatic, does not have root hairs at all; while *Elodea*, a submersed aquatic, has them only when the roots are in contact with mud.

The question arises as to what cells of the outer layer of the root produce root

hairs. Leavitt (46) reported in 1904 that in the grasses every cell may produce a hair. In *Azolla* (45), a water fern, he finds that root hairs arise only from short cells. This latter observation was also made by Savageau (68) upon *Naias* and by Kraemer (41), Van Tieghem (82) and Juel (37). Schwarz (73) and Miss Snow (75), however, think that there is no significance in the size of the mother cells. Schwarz gives the diameter of root hairs as varying from 0.011 mm. in corn to 0.050 mm. in *Trianea*. He estimated the number per square millimeter of root surface to be 10.9 in *Trianea* and 425 in corn, and the number per millimeter of root length to be 94 in *Trianea* and 4386 in *Scindapsis*.

Haberlandt (29) in 1887 was the first to show definitely that the root hair grows in length by the formation of additional wall only at the apex, although Nägeli in 1846 had included plant hairs along with pollen tubes, fungous hyphae, and algal filaments, as structures with apical growth.

As to the exact method of cell wall elongation there developed some difference of opinion. Wortman (88) in 1889 contended that it was by the addition of new layers on the inside of the wall at the tip, and a stretching of the wall simultaneously by increased turgor of the protoplast, keeping the wall at a constant thickness, but increasing progressively the volume of the cell. Zacharias (89) in 1891 obtained strong evidence that this is not the method, but that new wall material is inserted into the wall at intervals along the dome shaped tip, thus extending the wall, and that turgor of the cell is not the active factor in cell enlargement. This idea has recently been supported by the work of Ursprung and Blum (81) in 1921.

The most convincing evidence that the root hair does grow at the tip only is given by the experiments of Reinhardt (65) in 1892. He placed minute particles of red lead on the tip of the hair and watched their change of position as the hair grew. He found that they might become subdivided on the dome-shaped tip and invariably moved off of the dome as the hair grew, coming to rest on the side of the hair at the base of the dome, and remaining in contact with this part of the wall, while there was progressively more lateral wall added from the dome at the end.

Stiehr (77) in 1903 found several lines of evidence which indicate that the wall of the hair at the tip is different in composition from that of the rest of the hair. He found that it is more readily stretched and broken, as is shown by the fact that if the root hair is caused to burst the rupture occurs almost invariably at the tip. He also noted the form of the tip when particles were appressed to it, and describes it as appearing in this respect like a stick of warm sealing wax.

On the basis of his experiments on the curvature of root hairs in response to certain stimuli, as described below, Seidel (74) concluded in 1924 that the wall is more plastic at the apex of the root hair than at other points. This would perhaps be expected if the apex is the place where new wall material is being deposited. It is also in harmony with the work of Ziegenspek (90) in 1920, in which he found that the cell wall at the tip is of different chemical composition from that along the sides. He decided that it consists of a substance, called amyloid, which is a transitional carbohydrate, having some of the properties of starch. For instance, it turns blue with iodine, as does starch; whereas for cellulose to give this reaction acid must be added.

However it is not entirely certain that

in this case the amyloid is to be regarded as an intermediate carbohydrate between the soluble form in the cell sap and the cellulose of the fully developed cell wall along the sides of the hair. Miss Roberts (66), it is true, in 1916 reported that there was an inner layer of cellulose along the sides of the root hair, the outer layer of the wall being of calcium pectate. However, in 1921 Miss Howe (35) published a further investigation of the composition of the cell wall of root hairs in which she found no cellulose at all. In this way the root hair wall is strikingly different from that of partition walls and other external walls of the root proper. She also found that the outer layer of the lateral walls of the root hairs is of calcium pectate or pectose, but that the inner layer is of callose, which Miss Roberts found only at the tip of the root hairs of some species.

Considerable attention has been given the question of the location of the nucleus and its possible relation to root hair elongation. Mer (53) first reported the nucleus as moving along in the hair behind its tip. Haberlandt (30) found that in many plants it lies along the outer wall of the superficial cell, near the location of the bulge which developes into the root hair. He pointed out that in wheat and *Commelina*, while the nucleus does not lie against the wall, it is connected with it by numerous plasmatic threads. He also found that the nucleus, except in *Hydrocharis*, moves into the hair after it has attained a short length, and that it remains at a rather constant distance behind the tip. This distance varies for different plants. In peas it is about 13 microns and in pumpkin about 130 microns. He concluded from his study that the nucleus is an active agent in the controlling of the growth of root hairs. More recently Haberlandt's student, Windel (87), has added evidence to support his contention. He found that in mustard root hairs, the growth is at first apical, then basal, the nucleus moving accordingly. However, Kuster (44) in 1907 published his study upon the same subject, from which he concluded that there is no relation between the position of the nucleus and the growth of the hair. He believes it to be a mere coincidence that the nucleus should in some cases lie near to the point of origin of the root hair and attaches no significance to its presence in the hair. Miss Roberts (66) confirms this view and finds great variation in the position of the nucleus in hairs which are apparently behaving alike in their development.

Ziegenspek (91) has very recently found that the root hair of *Hydrocharis* does not grow at the tip, but that the amyloid is deposited intercalarly near the base, and suggests as the explanation of Haberlandt's observations that the nucleus in this plant does not move into the hair. Besides *Hydrocharis* Kuster noted seven other genera of aquatics in which the nucleus lies always in the cell proper, and three genera in which it may lie in the middle or lower part.

By studying the same hair for a period of time under normal living conditions the writer has obtained evidence that the nucleus not only may have no active part in stimulating or controlling the growth of root hairs but apparently may even passively retard elongation, or bring about the cessation of growth. It is, for instance, found that the nucleus may enter a hair and remain there for a short time during which the hair does not grow so rapidly; and then after it retreats to the cell proper again, the hair may resume its original rate of elongation. But the more convincing evidence is obtained from a study of so-called duplex hairs, that is in cases where two hairs emerge from a common base which is formed from a bulge

of a single cell. Such instances are not uncommon on roots of collards growing in simple calcium nitrate solutions. In this case there is just one nucleus for the cell proper and for the two hairs. In some cases the nucleus may move into the base only and remain there in a central position. In such cases as have been observed the two hairs then grow at approximately the same rate. Not infrequently, however, one of the hairs assumes a more rapid growth rate before the nucleus emerges. In this instance the nucleus almost invariably passes into the hair which is growing more rapidly. It is then observed that the rate of elongation is thereupon retarded and it may even cease elongating entirely, while the rate of the other hair is accelerated. After this other hair has, perhaps, attained a greater length than the one in which the nucleus is located, the latter has been observed to move over into the hair which is now growing more rapidly (fig. 1).

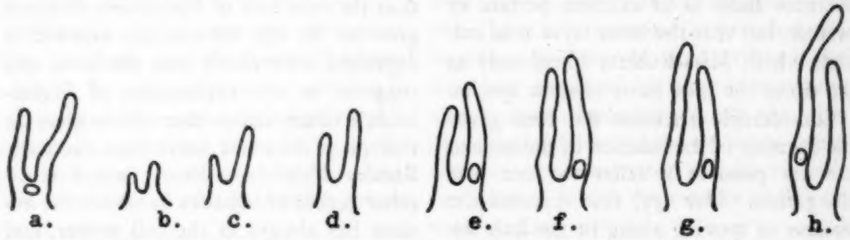

FIG. 1. DUPLEX ROOT HAIRS SHOWING THE RELATION OF THE POSITION OF THE NUCLEUS TO THE GROWTH OF THE TWO HAIRS

The series *b-h* represents different stages of the same hairs

It thus seems that the growth rate is likely to determine the position of the nucleus, rather than the position of the nucleus to determine the growth rate. However the position of the nucleus does seem to have some relation to growth rate, namely to retard or stop it, rather than to accelerate or start. This relation of the position of the nucleus to the rate of growth may be explained perhaps on the basis of the relation of the nucleus to protoplasmic streaming. The protoplasm of the root hairs of many plants may be seen to be in a state of circulation, flowing from the cell proper along the inner surface of the lateral walls, accumulating in the dome-shaped tip, and then flowing back again along another wall to the cell proper. There are also commonly seen currents which cut across the interior of the cell apparently forming strands of cytoplasm which pass through the vacuoles. There may also be one or more partitions of cytoplasm which completely separate one vacuole from another. In these partitions the protoplasm streams also. Furthermore the paths of streaming may be observed to be changing rather rapidly.

It is apparent that this streaming has a direct relation to the transportation of materials dissolved in the cytoplasm. It carries, for instance, materials for growth of the root hair from the cell proper to the growing tip. This material is chiefly no doubt some form of soluble carbohydrate, such as the sugars, or soluble polysaccharids like dextrin or inulin. At the apex of the hair it is changed into the insoluble amyloid, which is deposited in the cell wall. Whether this amyloid is later transformed into the pectic bodies of the outer layer of the wall or the callose of the inner layer, has not yet been deter-

mined. But whether either or neither of these alternatives is true, it is evident that the older portions of the cell wall are composed, with one exception, of material derived only from the root proper and not ordinarily of material from the outside. There is thus need of rapid transportation in the root hair if rapid elongation is to be effected.

The one constituent of the cell wall of the hair which may be, and probably for the most part is, derived from the exterior is calcium. The fact that root hairs, as is shown below, will not grow at all without the presence of calcium in the external medium indicates that it is used directly from this source for cell wall formation. But it is hardly conceivable that the calcium could enter alone. Theoretically it is possible for it to enter by exchange with potassium or some other cation, and doubtless some potassium and perhaps magnesium is liberated from the root in this way. But there is so much calcium absorbed, and furthermore so much carbon dioxide liberated from the root, that potassium liberation is not the only thing which happens at the surface of the root hair. There must be the absorption of some anions accompanying the calcium which are not received by exchange with potassium and such ions, and to compensate for the carbon dioxide which is liberated. From a calcium nitrate solution, for instance, nitrate ions are thus absorbed. They are not used apparently in the formation of the cell wall, so that they must be conducted into the interior of the root. But nitrate ions cannot travel alone. Neither can they be accompanied by the calcium ions with which they enter, for the calcium, as we have already seen, is deposited as calcium pectate in the cell wall, or as calcium oxalate in the vacuoles. Apparently the thing that happens is that in addition to carbohydrate being transported outward in the root hair, there is also a quantity of potassium oxalate and perhaps likewise potassium pectate, which meet the calcium nitrate entering the cell and undergo exchange with it so that the calcium pectate or calcium oxalate remains in the hair and the potassium and nirate ions travel back into the cell proper. There is thus a migration of carbohydrate molecules and ions of organic potassium or magnesium salts outward and of ions of inorganic potassium or magnesium salts inward. Thus we see that the root hair is a region of considerable physical and chemical activity, and that the streaming of the protoplasm greatly facilitates these changes.

As to the effect of the presence of the nucleus in a root hair upon the streaming, it is evident that its location part way along the hair, will modify markedly the paths of streaming. It usually lies, as shown below, surrounded by cytoplasm between two vacuoles. Its size is nearly such as to completely partition the interior of the root hair. There would thus be a tendency for the material to stream out to the cytoplasm surrounding the nucleus and then be diverted back along the opposite wall to the cell proper again without passing to the dome-shaped tip at all. Thus free movement of materials from the cell proper to the tip and back may be interrupted partially or almost completely. Unfortunately in the hairs in which the nuclear migrations and cessation of growth have been observed, as noted above, streaming of cytoplasm cannot be seen, so that confirmation of this interpretation by direct observation has not as yet been made. It is thus seen that there is at least a possible explanation as to how the nucleus may operate as a passive causal agent in the retardation or cessation of growth of these root hairs.

The reason why the nucleus should move

from the cell proper into that hair of the duplex which is growing more rapidly, and should migrate from a slow growing hair to a more rapidly growing one may, perhaps, also be associated with protoplasmic streaming. The nucleus is known to move in other cells having protoplasmic movement, such as leaf cells of *Elodea* and *Vallisneria*. Whether it is carried along passively, or whether it is activated by the same principle that activates the plastids and cytoplasm is not yet known. Sokolowa, after a careful study of nuclear position and protoplasmic streaming, decided that they are interrelated. He thinks that there is an exchange between the nucleus and the stream.

Protoplasmic streaming in root hairs has been observed for many years. It is especially evident in the large root hairs of such aquatics as *Hydrocharis*, *Trianea*, and *Limnobium*. Here it is so rapid that under high magnification it takes on the appearance of the surging of the surf. Reinhardt (65) noted that upon immersing hairs to coat them with red lead, growth ceased. He also noted that protoplasmic streaming stopped. After a time both the streaming and the growth were resumed approximately simultaneously, which indicates, as suggested above, that streaming does facilitate, at least, if not condition, root hair elongation. In the small root hairs of most seedlings protoplasmic streaming is not usually apparent. Mrs. Farr (25) has reported it to be conspicuous in oats, but it is not evident in collards, rice, and similar root hairs, owing possibly to its absence, but also perhaps to the greater degree of refraction of the more highly curved surface of the smaller hairs, or to the absence of particles in the protoplasm. That protoplasmic streaming does occur in these hairs is indicated by the rather rapid change in the arrangement of the vacuoles.

The vacuolar system of root hairs has not been extensively studied. Mer first (1880) referred to them. Miss Addoms (1) describes the development of a root hair as regards its vacuoles as follows:

> In a very young root hair the protoplasm is dense and almost devoid of vacuoles. As the root hair grows, the protoplasm becomes less dense, vacuoles form and enlarge, and the cell is apparently at the height of its usefulness as an absorbing organ. The vacuoles continue to enlarge and begin to coalesce, and the protoplasm is crowded more and more toward the outside of the cell, so that finally it is but a thin film separating the cell sap from the cell wall, and the root hair is of little value to the plant.

Her interpretation of the efficiency with which root hairs function as organs of absorption, based upon the intracellular organization, is in harmony with the experimental evidence of Popesco (64), which indicates that the older hairs, that is, the longer ones, do not function in absorption.

Strugger (78) finds in barley, as does the writer (21) in collards, that the most typical arrangement of vacuoles consists in a terminal vacuole between the protoplasm surrounding the nucleus and that in the dome-shaped tip (fig. 2 (a)), and a basal vacuole, which is an extension of the vacuole of the cell proper up into the root hair to the vicinity of the nucleus. Strugger finds, however, that if the hydrogen ion concentration of the medium is increased slightly, for instance, from pH 6.6 to 6.3, the apical vacuole disappears. If it is increased still more, that is to 6.2, many small vacuoles appear. If changed to pH 6.1 secondary vacuoles disappear. A change now to slightly greater acidity, pH 6.0, gives the normal condition again. By increasing the acidity farther the cycle is repeated once, reaching a lethal acidity at pH 5.6. He finds a similar bimodal curve for streaming with a maximum rate at pH 6.15. This indicates a remarkably

high degree of sensitivity to small changes in the reaction medium. No data are given as to the percentage of root hairs in each solution in which the organization given as typical occurs. It is also to be observed that Strugger used roots which were severed from the rest of the seedling and then transferred to the solution. It has been found (12) that transfer of the root to the solution from air has a marked effect upon the development of the hairs, intervals. No relation between vacuolar organization and hydrogen ion concentration was detected. In each solution there was a considerable range of variation in this regard. Even in the same hair there was a change found (fig. 2 (b)) from time to time, changing visibly in the course of one or two minutes. It was furthermore found (fig. 2 (c)) that the development of an isolated vacuole in one of the hairs of a duplex may be accompanied by cessation

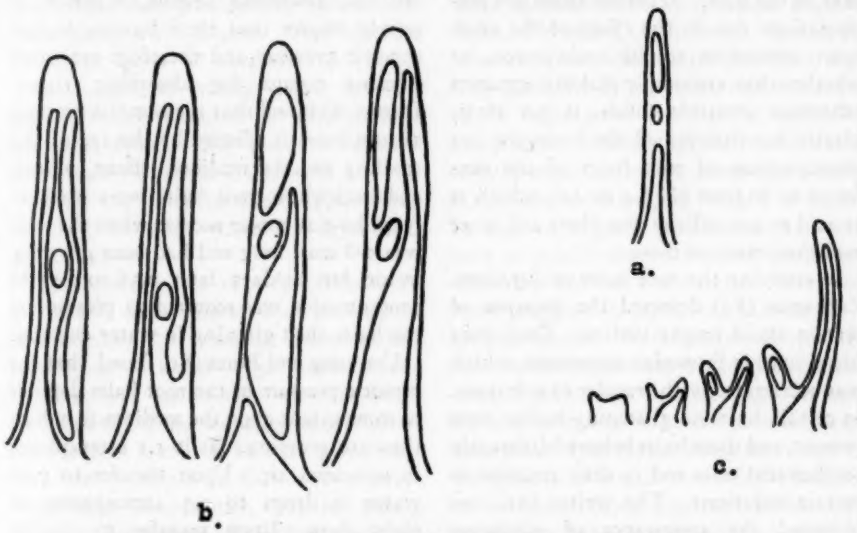

FIG. 2. ROOT HAIRS SHOWING RELATIVE POSITIONS AND VARIATIONS IN VACUOLES

The series (*b*) was drawn from the same hair at intervals of a few minutes. The series (*c*) also shows the vacuolar condition during the development of a duplex hair.

which varies with time after immersion. It would be surprising if severing the root from the seedling would not have even a greater effect upon the behavior of root hairs.

The writer (21) has studied in collards the vacuolar changes in root hairs which developed on the attached root some hours after immersion in solution of simple calcium salts. They were studied over a range of hydrogen ion concentration from pH 4.5 to 11.5 at one or one-half pH unit

of growth, while the other hair with a vacuole formed as an extension of that of the cell proper would continue to elongate at the normal rate. This indicates that the vacuoles may operate in much the same way as the nuclei in setting up cross currents, due to their position, which divert the main stream of materials from the tip by means of a short cut back to the cell proper, and thus bring about retardation or cessation of growth.

Schaede (71) has studied the root hairs

of *Hydrocharis* rather intensively, using a wide variety of intravital stains. He used protoplasmic streaming as an index of the normal condition of the cell. He has been able to compare the effect of different dyes on the cell and found that most of them, with the exception of Chrysoidin, cause alterations, which he regards as injurious or lethal. He also found that the cytoplasm is basic when alive and acid when dead. Upon staining crystals appear in the hair. Whether these are precipitations due to the effect of the stain upon otherwise soluble substances, or whether they are simply making apparent otherwise invisible solids, is not clear. Martin has determined the hydrogen ion concentration of root hairs of the sunflower to be from pH 4.4 to 4.0, which is as acid as any cells of the plant and more acid than many of them.

In studying the root hairs of *Lepidium*, Zacharias (89) detected the presence of certain small bright bodies. They were found to be in Brownian movement, which was accelerated with transfer to solutions. In certain hairs no glistening bodies were present, and these hairs behaved differently to chemical tests and in their reaction to certain solutions. The writer (21) has observed the appearance of glistening bodies in hairs of collards, but only when growing in very alkaline solutions.

The osmotic pressure of the root hairs of ordinary plants has been measured by the plasmolytic method, that is, by determining the strongest solution which will not cause shrinkage of the protoplasm. Miss Roberts found that root hairs of different species were plasmolyzed by sucrase from 0.22 M to 0.4 M concentrations after growing in air, and that in solutions they maintain an osmotic pressure 4 to 6 atmospheres higher than the medium. Ursprung and Blum (81) found an osmotic pressure of 1.1 atmospheres, the lowest that they observed in any of the cells of the plant. Miss Addoms (2), however, finds that the root hairs are not plasmolyzed as readily by either salts or sugars as are other cells of the root, especially the root cap and the cortex. She finds, for instance, that 0.8 M sodium chloride or 0.5 M cane sugar will affect the latter tissues, but not the root hairs. Popesco (64) obtained similar results with plasmolysis and argued, therefore, that root hairs are not absorbing organs, whereas it simply shows that they have a higher osmotic pressure and therefore are more efficient organs for absorbing water. Ohga (58) found that the osmotic pressure of root hairs is affected by the age of the seedling and the medium. Bean, wheat, and buckwheat root hairs were plasmolyzed by 0.24 molar sucrase when the root was 5–8 cms. long and had been growing in air, but 14 days later 0.36 to 0.54 M concentration was required to plasmolyze the hairs then growing in water cultures.

Ursprung and Blum (81) found that the osmotic pressure of the root hairs depends to some extent upon the medium in which they are growing. It is 1.1 atmospheres in saturated air. Upon transfer to pure water it drops to 0.3 atmospheres in eight days. Upon transfer to 0.2 M sucrose it rises to 5.3 atmospheres in one day. The plant thus has the ability to adjust the osmotic pressure of root hairs to approximate that of the surrounding medium. It should be pointed out, however, that this adjustment is made, not by changing the osmotic pressure of a given root hair, but by sending out new root hairs in the new concentration, having a different osmotic pressure. Halophytes, that is, plants which grow in soil high in salt content, such as seaside plants, have a much higher osmotic pressure in their root hairs. Hill (34) found that *Salicornia*, for instance, will not be plasmolyzed by

5.8 per cent sodium chloride, whereas ordinary plants growing in cultivated soils cannot resist more than 1.5 per cent.

REACTIONS OF ROOT HAIRS TO EXTERNAL CONDITIONS

Root hairs are found to respond to external conditions in various ways. In the first place certain conditions will permit their development, while they will not arise at all under others. Under some conditions they burst; under others their protoplasm is coagulated. They also are found to curve in response to certain stimuli, and to change their form by varying their diameter or direction of growth. Finally they grow at different rates under different conditions.

Pfeffer (63) was the first to observe the bursting of root hairs by hypotonic solutions.

Zacharias (89) in 1891 found that the cell wall might burst and growth be continued by the formation of a new inner membrane. Klemm (39) studied the bursting and contraction of cells under various conditions, including observations on the root hairs of *Trianea*. He found that the protoplasm does not contract with high temperature, but in young hairs it does contract at low temperatures. He found that low concentrations of acids have an explosive effect on these hairs. Stiehr (77) observed bursting in root hairs of timothy when placed in 0.15 per cent to 1 per cent solutions of several common salts.

Klemm (39) observed coagulation of protoplasm of hairs of *Trianea* in 0.1 M nitric acid or oxalic acid. Miss Addoms (1) has made the most extensive study of various substances in bringing about the coagulation of the protoplasm of root hairs. She attributes it in part to high degree of acidity of the solutions, ranging as they did from pH 3.94 to pH 3.47, or to high concentration of the salts, using 0.1 M solutions of potassium, sodium, calcium, magnesium, zinc, and aluminum salts, aluminates and cyanides. She has also found that ultraviolet light may bring about the coagulation of root hairs.

The effect of light upon root hairs has been considered, especially in connection with the question of the proper conditions for their production. Schwarz found no effect (73). Constantin found that root hairs develop more in darkness than in light. Devaux (1888) found that roots in water grew faster in the dark, but that they bore few or no hairs, whereas roots in the light grew less rapidly, and bore many hairs. Later (1891) he found that in some grasses, as *Lolium*, there was a daily periodicity of root hair length in light, so that each day's production formed a cone or spindle shaped mass of root hairs. This showed that not only are more root hairs produced in light, but they attain a greater length. Went's experiments were not convincing. Pethyridge (62) on the other hand reports that light retards root hairs of wheat and oats in water cultures. Miss Snow (75) found little difference in the number or length of root hairs in light or darkness. Seidel (74) reports that only in intense light is root hair growth inhibited. Jeffs (36) made a definite study carefully measuring the elongation of root hairs in saturated air using different intensities of illumination. He found no effect of light so long as temperature is kept constant. It thus seems that much of the earlier work indicating a definite effect of light on root hair production and growth is not supported by more recent and more detailed observations.

The first definite study of the effect of temperature on root hair production was made by Miss Snow (75). She found that wheat produces numerous hairs between 4.5° and 11.5°C., fewer between 16.0° and

29.5°C., and none at higher temperatures. Corn likewise produces none above 27.0°C. Jeffs (36) studied the effect of varying the temperature upon the rate of elongation of a single hair. He found that a very slight change, two or three degrees, in either direction caused either a temporary or a permanent cessation of growth. In many cases where growth was resumed, there was apparent an enlargement of the root hair during the period of adjustment to the new temperature. Schwarz (73), Pfeffer (63), Went (85), and Miss Snow all agree that contact in itself is not a factor in root hair production, but that the effect is a chemical one.

The most extensive study of root hair production has been upon the effect of water and air respectively. Martin found them shortest in water, longer in soil and longest in air. Mer (53), who was one of the first to consider this question, attributed the lack of root hairs on many species in water to the stimulating effect of the medium upon root elongation. He found that roots in air have root hairs developing much nearer the tip than those in water; that is, the region of elongation of the root is greater in water. He concluded therefore that the production of root hairs was a response to inhibition of root elongation. He also pointed out an inverse relation between root-hair production and production of lateral roots which was later confirmed by Constantin (4) and Lesage (48). Miss Snow found that corn, which normally does not produce root hairs in an aqueous medium, may be induced to do so by increasing the oxygen supply of the water in which it is grown. Vöchting (83) found that a reduction of the O_2 content of the air to 3 per cent inhibited the production of root hairs in water. Surprisingly few species of plants have been reported as producing root hairs in water. The writer has compiled (12) a list from the literature, and added several, making a total of only 87 species. It is not considered, however, that this list is by any means complete. Many plants, which have been reported as not producing root hairs in water, will undoubtedly be found to do so, when the proper adjustment is made of oxygen content, hydrogen ion concentration, osmotic pressure, and chemical composition of the solution. Mer (54) found that even onion roots will produce root hairs if left in air long enough.

Not much evidence has been accumulated as to the effect of highly concentrated solutions, that is solutions of high osmotic pressure of the medium, upon root hair production. Patschovsky (60) found that rhizoids of *Chara* are inhibited by an 8 per cent Knop's solution, whereas they grow well in a 1 per cent solution. The writer (13–24) has studied the rate of elongation of root hairs of collards in different concentrations of calcium chloride and calcium nitrate. He found that above the optimum concentration, about 0.020 molar solution, the rate falls off at first rapidly with increased concentration, and then more gradually, reaching a maximum concentration in the case of chloride at about 0.185 molar solution. If, instead of adding additional salt to the optimum concentration, which is about equivalent in osmotic pressure to a 1 per cent Knop's solution, sugar be added, it is found that a similar drop in rate of growth occurs to that which is obtained by adding equimolar amounts of the salt. It is therefore concluded that above a certain concentration osmotic pressure of the solution does have a retardative effect upon root hair elongation.

Krassnow (42) and Gerneck (27) both found that roots were much more abundantly haired in $Ca(NO_3)_2$ than in KNO_3.

Michcels (57a) found root hair elongation more rapid in nitrate than in chloride. Hansteen (31), Coupin (5), Kuster (44), Trelease (79), and the writer (14), all find that calcium is apparently necessary for root hair production. Hansteen has been the most ardent and insistent advocate of this view in repeated papers (31, 32). Kisser (38) has, however, demonstrated it in the most convincing manner. He supported seedlings in a chamber in such a way that no contact of the seedling was made with substances containing calcium. For this purpose he found it necessary to use special calcium-free cloth and glass. In this case the root grew, but no root hairs were formed. If, however, the slightest trace of calcium came in contact with the root, root hairs emerged. Hansteen (31) found that the calcium must be absorbed from the exterior in order for root hairs to appear. He grew seedlings with one root in a calcium solution and the other in a solution of some other salt, and found root hairs only on the former. Only one reference (49) is found in the literature to root hairs developing in solutions of single salts other than those of calcium, and in this case it is not unlikely that impurities may have been present. Both Kisser and Hansteen found that magnesium, potassium, and pure water suppress development of root hairs. The writer has confirmed these findings for pure water. The significant feature with regard to calcium in relation to root hairs seems to be that it is utilized directly in cell wall formation, and is in fact, the only constituent of the cell wall which is not synthesized within the plant.

Sachs (67) was the first to attempt an explanation of the curving of root hairs around soil particles. He attributed it to thigmotropism, that is, a response to contact with soil particles. Schwarz (73) concurred in this interpretation and noted that such curvatures do not occur in water or in saturated air, where no solid bodies come in contact with root hairs. Jost and Pfeffer, the leading plant physiologists of the last part of the last century, accepted this interpretation also. No further studies were, however, made until very recently, when by a careful and thorough investigation Kurt Seidel (74) found that this interpretation is incorrect, and that the curving of root hairs in soil is a chemotropism, and not a thigmotropism.

Seidel noted that root hairs of lamb's quarters, *Chenopodium*, curve toward cast-off pieces of the root cap of the same plant. He then used various parts of this and other plants, fresh and decomposed, also various organic and inorganic compounds, and finally purified quartz crystals alone. He found no response at all to the latter. He did find that *Chenopodium* gives a positive curvature toward all soluble phosphates, while salts of other simple cations, sodium, iron, potassium, calcium, magnesium, ammonium, etc., gave no effect. Neither oxygen nor carbon dioxide brings it about; neither does acidity or alkalinity. The minimum threshold concentration for potassium acid phosphate is 0.0025 to 0.0040 per cent. The maximum was about 2 per cent, in which case 33 per cent of the hairs reacted, and the others appeared injured. Seidel demonstrated by a number of ingenious experiments that the normal direction of root hairs at right angles to the root is not a matter of mutual repulsion or attraction. When he fitted a glass sleeve over the root, for instance, the hairs grew out normally above and below it without curving. He also observed that the root hairs on the concave side of a curved root are straight and cross each other, showing no mutual interaction.

With regard to other species, he found

that *Rheum*, *Brassica*, *Lepidium*, and *Plantago* are like *Chenopodium* in being positively chemotropic to phosphates. Oats, wheat, barley, and millet react, however, to ammonium compounds instead of phosphates. *Agrostemma*, another grass, reacts, on the other hand, only to nitrates. *Lychnis cornonaria* and *Oenothera*, the evening primrose, react both to nitrates and phosphates. *Ornithopus* reacts to phosphates and to all potassium compounds. No instance was found of a negative chemotropism, that is, a curvature away from a substance. All of the plants named above react also to soil particles; but root hairs of *Urtica* (a nettle), *Nicotiana* (tobacco), and *Verbascum* (mullein) react neither to soil particles nor to salts. He concluded that the region of sensitivity and the region of activity were both located in the tip of the root hairs. He found no correlation between the specific reaction of the plant to these substances and its momentary need of them. There thus seems to be no possibility of a teleological explanation of these reactions. It is apparent, however, that they tend to lead the root hair in its growth in the soil in the direction of increasing concentrations of nutrients, and to become appressed to soil particles, along which these solutions migrate, and from which their content is replenished by action of root hair secretions and by bacterial processes.

THE RATE OF ELONGATION OF ROOT HAIRS

It is rather surprising that with all the study of root hairs in almost every other possible aspect no attention has been paid until now to the rate of elongation. The only reference in the literature, prior to the work of the writer is that of Reinhardt in 1892 (65), who determined the increase in length of root hairs of *Lepidium* during a period of 24 hours, and records his results by a simple statement that they grow from 0.3 to 0.7 micron per minute, and may attain a rate of 0.9 micron. Sokolowa (fig. 3) drew the form of the tip at 1 minute intervals for 12 minutes and thus showed that the tip does not grow symmetrically but that the area of enlargement shifts from side to side slightly. The writer has found, by measurement, that while the rate is fairly constant over hourly periods, it varies considerably for ten minute intervals. The writer first measured (11) the rate of elongation of root hairs produced on cuttings of *Tradescantia fluminensis* growing in Knop's

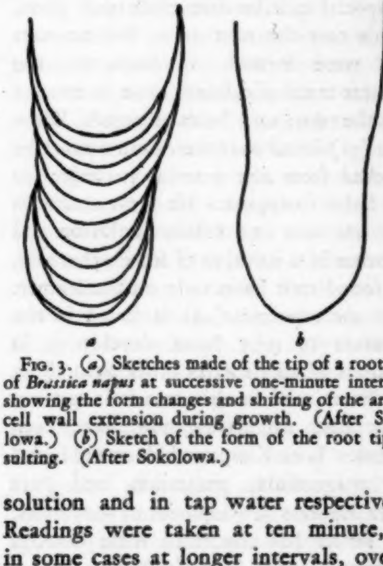

FIG. 3. (*a*) Sketches made of the tip of a root hair of *Brassica napus* at successive one-minute intervals, showing the form changes and shifting of the area of cell wall extension during growth. (After Sokolowa.) (*b*) Sketch of the form of the root tip resulting. (After Sokolowa.)

solution and in tap water respectively. Readings were taken at ten minute, or in some cases at longer intervals, over a period of several hours. It was found that the rate of elongation was more rapid in tap water than in Knop's solution. Because of the variability of tap water, and the complexity of the nutrient solution, these results were not of great significance.

Seedlings have, however, proved more suitable for such studies, inasmuch as they can be grown in small chambers on the stage of the horizontal microscope.

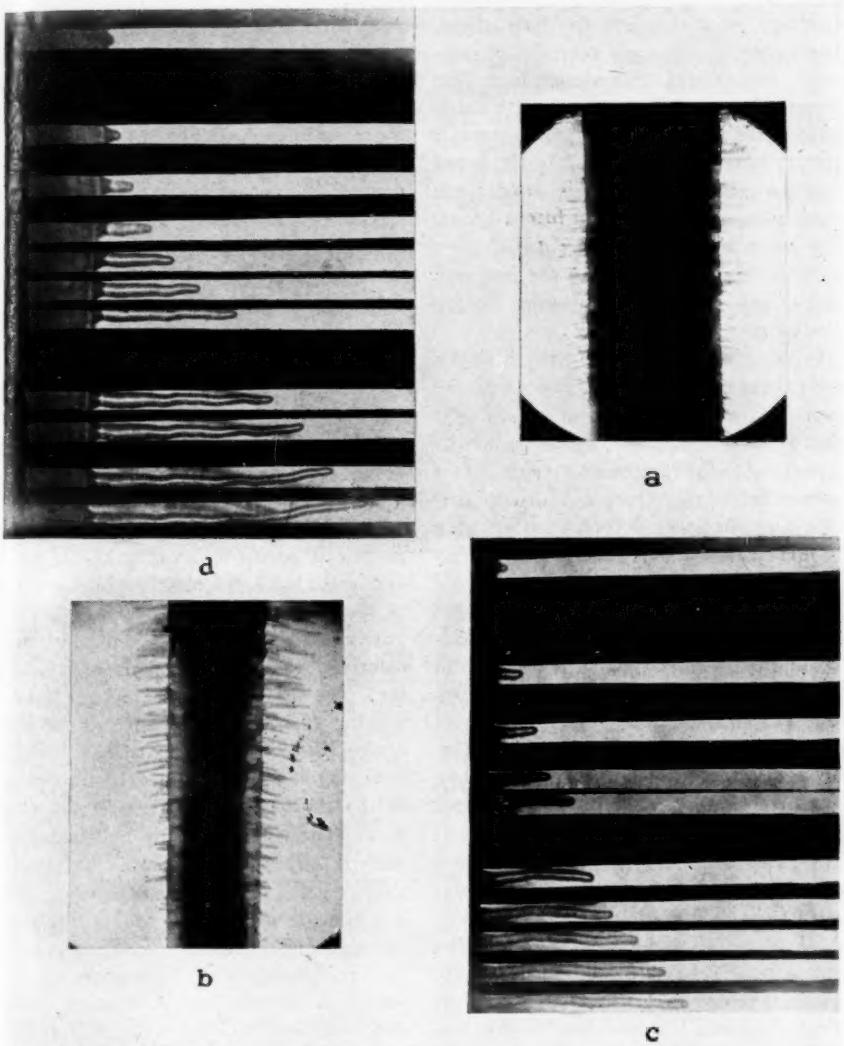

FIG. 4. (*a*) Photograph of the radish root in the root hair zone. (*b*) Photograph of the popcorn root in the root hair zone. (*c*) Root hair of popcorn photographed at 15-minute intervals. Spaces between the upper five photographs show lateral movement. The lower five show root hair elongation only. (*d*) Root hair of radish photographed at 15-minute intervals for $2\frac{1}{2}$ hours. The spaces between the upper seven photographs show the amount of lateral movement during each interval. The lower four show root hair elongation only. (After Jeffs.)

Jeffs (36), working under the writer's direction, was the first to study these, using corn, radish, and mustard in saturated atmosphere. He determined first the grand period of growth of these hairs, taking readings at fifteen minute intervals for periods up to ten hours. He found that the grand period extends, under these conditions, for from ten to fifteen hours. The curve is of the typical sigmoid form with an acceleration during the first two hours, and finally a retardation, during two or three hours.

In the case of root hair growth, however, there seems to be a definite explanation of the acceleration during the first part of the grand period of growth, which is peculiar to the root hair situation. It is to be observed that this period of acceleration does not occur in root hairs growing in aqueous media (11, 14, 15, 16, 17). In water root hairs elongate at a constant rate from the start. It has been noted above that root hairs in air occur much nearer the tip of the root than they do in water; and Jeffs (fig. 4) found that this involved an overlapping of the region of root hairs with the region of root elongation. That is, the root hairs which are just emerging in air, are on the upper portion of the region of root elongation. This is shown by the fact that these very young root hairs are carried along downward very slowly during the first two or three hours of their development. The rate at which they are thus carried along, which is referred to as their lateral movement, becomes less and less during this period, so that at the close of the interval they cease this movement. It is observed that this retardative lateral movement is coincident with the acceleration of their elongation. It is thus apparent that as the epidermal cell decreases its rate of elongation vertically, it increases its rate of elongation horizontally, that is the elongation of its root hair. Thus it appears that cell enlargement may proceed during this process at a rather constant rate. The absence of such a period of acceleration of root hair elongation for roots in water simply means that the cells or the root have already ceased vertical elongation in the region which is producing root hairs. The graph for the grand period of growth for root hairs in water is then not the typical sigmoid form, but consists of a rather straight line with, in some cases, a retardation to zero near the end of the period.

An intensive study has been undertaken by the writer (14) of just one variety, Georgia collards, of just one species of plant, *Brassica oleracea*. To this same species belong cabbage, cauliflower, kohlrabi, Brussels sprouts, etc. Seedlings are chosen as nearly as possible of the same age, and placed in a chamber on the stage of the horizontal microscope, in such a position that the root is immersed in a solution, while the shoots develop in the air. The solution in the chamber is kept flowing at a rather constant rate, so that during the period of the experiment, which is 16 hours, there is practically no change in the chemical composition of the solution. The solutions thus far used have been of single calcium compounds, namely, the hydroxide, chloride, and nitrate. The experiments were performed in duplicate for each molar and hydrogen ion concentration. Previous to insertion of the seedlings a solution of known molar concentration and known degree of acidity or alkalinity was aerated with carbon-dioxide-free air, so that it contained an abundant supply of oxygen, but little or no carbon dioxide. The entire experiment was performed in a dark room of reasonably constant temperature. The only illumination consisted of a very weak red light which was used during the period

of taking observations, namely, between 12 and 16 hours after insertion.

Measurements of the length of 8 to 16 root hairs on each root were made at ten minute intervals during three hours beginning 13 hours after insertion of the root in the solution. The root hairs measured were such as appeared after ten hours

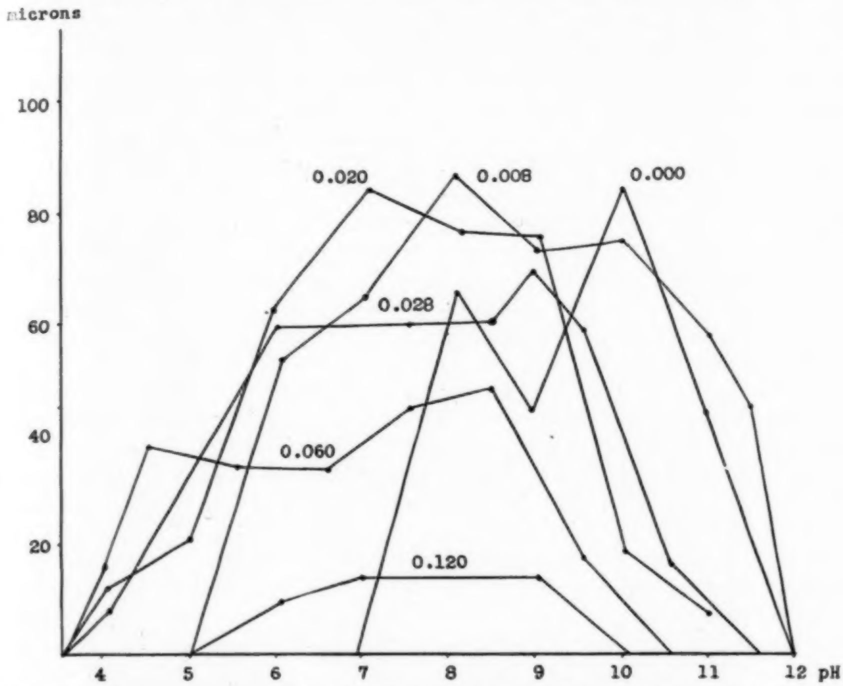

FIG. 5. GRAPHS REPRESENTING THE RATE OF ROOT HAIR ELONGATION OF COLLARDS IN SOLUTIONS OF DIFFERENT MOLAR CONCENTRATIONS OF CALCIUM CHLORID, PLOTTED ALONG THE SCALE OF HYDROGEN ION CONCENTRATIONS. THE GRAPH LABELED 0.000 IS FOR CALCIUM HYDROXIDE

immersion, that is, after the root had become entirely adjusted to the solution.

The determination of the rate of elongation of root hairs in calcium hydroxide is of interest because it is the simplest solution in which they will grow at all. It is highly interesting, therefore, to find that in this simplest solution they have been found to grow faster than in any other medium so far studied. It was definitely shown (14) that they will not elongate in distilled water during the period studied. In fact few root hairs are produced after immersion in pure water. Inasmuch as the different molar concentrations of calcium hydroxide differ in the degrees of their alkalinity, the constitution of these solutions may be determined either volumetrically or colorimetrically. Both methods were employed. The initial study with calcium hydroxide was made in 1926 (14), and the study was repeated the next year (20), completely confirming the previous results.

It was found that the rate of elongation rises from zero at pH 7 (fig. 5), neutrality, to a first optimum at pH 8, and then drops to a median minimum at pH 9.0, rising to

a second optimum at pH 10.0 and then at higher concentrations dropping to zero at pH 12.0. The rate at pH 10.0 is the most rapid, being an average of 97.0 microns per hour for all root hairs measured, and in the case of one hair attaining a rate of 114.2 microns per hour, which was the most rapid growth obtained for any hair of the 3500 or more so far measured in this and other solutions.

It is perhaps significant to observe that the simplest solution in which root hairs will grow supports the most rapid growth. While other solutions may be found later which will give still more rapid elongation, yet this indicates the great importance of calcium to root hair elongation, and perhaps the lack of a necessity that any other mineral element be present on the outside. That calcium is utilized directly in root hair elongation is indicated by the fact that it is not the lowest concentration of calcium hydroxide that supports the most rapid growth. It is apparently the highest concentration which can overbalance the inhibitory effect of the hydroxyl ion. This is further indicated by a comparison of root and root hair elongation in calcium hydroxide. Root elongation rises to an optimum at pH 8.0 or 8.5, above which it drops off gradually to zero without rising to a second optimum. This indicates that at least in these dilute solutions the calcium does not penetrate into the interior of the root, but is consumed largely or entirely by the superficial cells, especially the root hairs; while the hydroxyl ions do penetrate and in the more alkaline solutions have a retardative effect upon root elongation.

The bimodal graph for variations in hydrogen ion concentration has been secured for a large number of biological reactions, especially those involving growth. Salter and McIlvaine obtained it for the growth of wheat seedlings, Hixon for the germination and growth of seedlings of various plants, Olsen for the growth of plants to maturity, Hopkins for the development of a fungus, *Gibberella*, Cole for the growth of roots of corn seedlings, Arrhenius for the extension of leaf areas and growth of plants in water, sand, and soil, Cohen and Clark for the number of viable bacteria of *Bacillus dysenterica*, Robbins for the growth of fungi and reactions of potato tubers, McSwiney and Newton for reactions of smooth muscles, Herčík for root growth of *Pharbitis*, and Hopkins for locomotion of *Amoeba*. Similar bimodal curves have been obtained with non-living colloids, with regard to their swellability, precipitation, viscosity and other properties. Loeb demonstrated that in the case of certain proteins the median minimum of these curves was located at the hydrogen ion concentration of the isoelectric point of the protein. It has therefore been concluded by Robbins and others that the depression in the pH graph for growth was indicative of and a response to the isoelectric point of the constituent proteins. Pearsall has found in some cases trimodal and multi-modal graphs for the response of plants to changes in pH, and suggests that the various depressions in the graphs indicate the respective isoelectric points of the constituent proteins.

It is obvious that a much more extensive study is necessary in order to ascertain the growth rate of root hairs in different solutions of other calcium compounds than the hydroxide. With the hydroxide, hydrogen ion concentration is proportional to molar concentration, and hence there are only two variables, concentration and rate of elongation. With simple calcium salts, however, the hydrogen ion concentration may vary without changing the molar concentration, and vice versa, so that there are three variables:

hydrogen ion concentration, molar concentration, and rate of elongation.

The lowest molar concentration of calcium choride (16) studied thoroughly was 0.008. It gave a pH range from 5.9 of 0.028 M had a range of 3.9 to 10.4, with optima at 6.5 and 9.0, the alkaline optimum in this case being the greater, while at lower concentration of the salt it was the lesser. In 0.060 M the range is

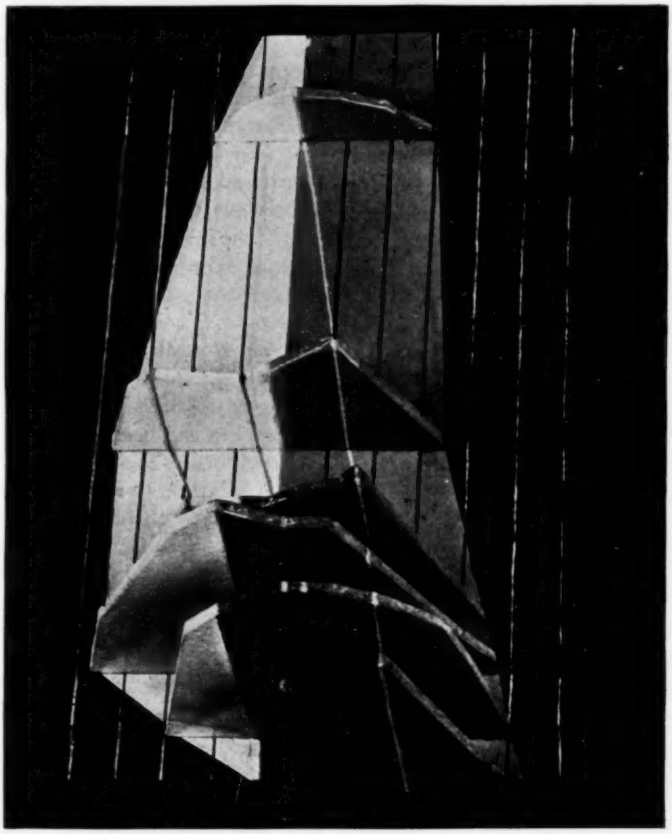

Fig. 6. A Model Showing Graphs Similar to Those Given in Figure 5 Disposed upon a Plane at Distances Coördinate with the Molar Concentrations

The graphs here used are based upon the most rapid root hair measured, rather than on the average. The result is not substantially different, except that no median minimum is apparent in 0.008. This model shows that the optima and the median minima fall in approximately straight lines.

to 11.4 with a distinct optimum at pH 8.0 and a lower and less distinct optimum at 10.0 (fig. 5). A concentration of 0.020 molar gave a range of 3.4 to 11.4 with optima at 7.0 and 9.0. A solution 3.5 to 9.5, with the lesser optimum at 4.5 and the greater at 8.5. In 0.120 M calcium chloride the range is 6.0 to 9.0 with just one optimum at 7.0.

It is apparent that these data can be

better correlated if they be plotted in three dimensions. A model was therefore constructed (fig. 6) representing the rate of elongation plotted against pH by erect cards, standing on a platform, the two dimensions of which are spaced to correspond to the hydrogen ion concentration and the molar concentrations respectively. It is found by this arrangement that the alkaline limit falls in a straight line, and

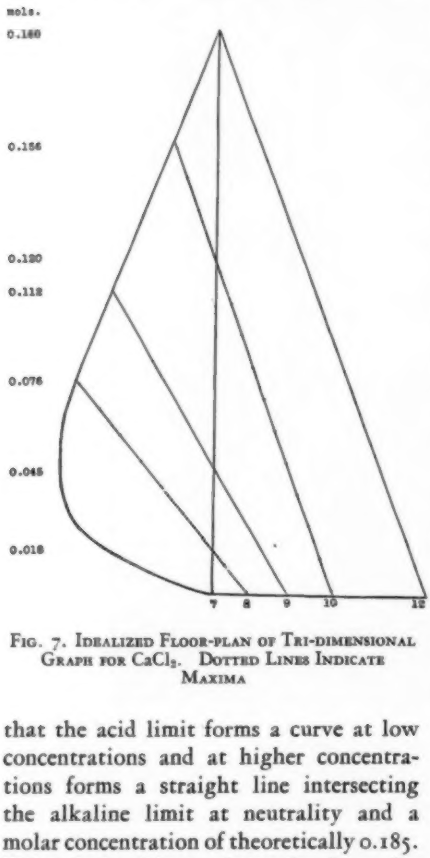

FIG. 7. IDEALIZED FLOOR-PLAN OF TRI-DIMENSIONAL GRAPH FOR $CaCl_2$. DOTTED LINES INDICATE MAXIMA

that the acid limit forms a curve at low concentrations and at higher concentrations forms a straight line intersecting the alkaline limit at neutrality and a molar concentration of theoretically 0.185. This relationship can better be shown by a map or floor-plan of the model (fig. 7). In this also it is shown that the alkaline optimum and the acid optimum form straight lines, with the median minimum between. It need scarcely be pointed out that it is necessary to incorporate the graph for calcium hydroxide in these models and maps inasmuch as it may be looked upon as representing zero concentration of the salt.

From this model and map there can be readily pointed out the relationship between the effect of the respective ions present namely, Ca, Cl, H, and OH, and their mutual interaction. For instance, it is seen that no growth occurs in acid solutions of low calcium content. This is in harmony with the agricultural experience of the inadequacy of acid soils low in calcium, and indicates a possible explanation of the beneficial effect of adding calcium to an acid soil, if by so doing the root hair elongation is changed from zero to the maximum rate in any concentration of this salt, namely at a concentration of about 0.010 and neutral or slightly alkaline solutions. The growth of root hairs in acid solutions, with moderate calcium present, indicates that the latter ion has an antagonistic effect upon the hydrogen ion. This is also in harmony with the results of others upon studies in plant development. At still higher concentrations of the calcium, however, a new relationship is brought out, namely that the hydrogen ion does not have an antagonistic effect upon the calcium ion, that is, in higher concentrations of calcium chloride no growth occurs in very acid solutions. In like manner relationships may be pointed out between the chlorine ion and the hydroxyl ion on the alkaline side. The interpretation here is however complicated by the difference of interpretation of alkalinity as due either to the presence of the OH ion in excess or simply to the decrease in amount of free hydrogen ion. It is also complicated by the fact that the calcium seems to play a direct part in the growth of the root hair, and

the rôle of the chlorine is thus probably secondary. The effect of the anion upon root hair elongation can thus better be ascertained by a comparison of the one anion with another, such as chloride with nitrate. This will be done below.

The results for the growth of collards in calcium nitrate are given in the accompanying figures (8 and 9). It is apparent that at low concentrations the pH graph however, some differences. The maximum rate is slightly less in nitrate than in chloride. The range does not extend quite so far on the acid side in nitrate; but it is apparent that the antagonism of calcium for hydrogen ions is greater in the nitrate than in the chloride. That is, the addition of less nitrate to an acid solution is necessary in order to permit it to produce root hairs, than of chloride.

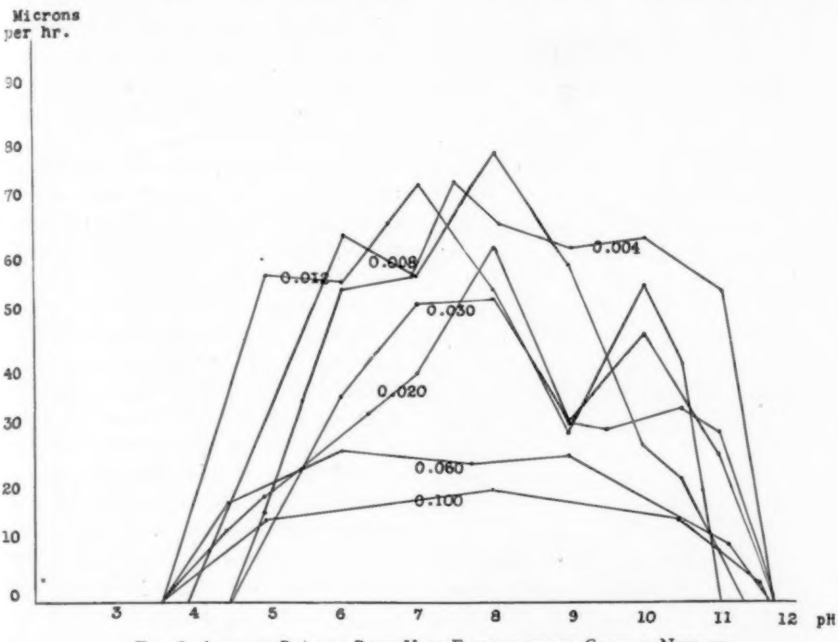

FIG. 8. AVERAGE RATE OF ROOT HAIR ELONGATION IN CALCIUM NITRATE

for nitrate is trimodal, for medium concentrations it is bimodal, and for high concentrations it is monomodal. The relationship becomes, however, perfectly clear when we consider the data in terms of the three dimensions.

The results for nitrate approach very closely to those for chloride (fig. 10) and indicate that the cations have doubtless much greater effect upon root hair elongation than do the anions. There are, By the construction of similar maps to these for each of the nutrient and non-nutrient anions it is hoped that a clear picture may be presented of the effect of each constituent of the nutrient and then of the soil solution.

It is important to notice the very wide range of hydrogen ion concentration in which the root will produce root hairs. This is not to be taken as an indication of the ability of root hairs to adjust them-

selves to a wide range of conditions. On the contrary, they are extremely sensitive to changes in the medium, as was pointed out above in regard to temperature, and as will be shown below. But it does show clearly that the root has a great ability to adjust itself to a wide range of conditions, and to produce root hairs in solutions of many different constitutions. The prime requisites seem to be that calcium be present, and that the minimum amount of calcium supplied be greater the greater the acidity of the solution, that the solution shall not be too strongly alkaline or acid, and that the concentration of the salt must not be too high since the resistance to acid and alkali is less at high concentrations.

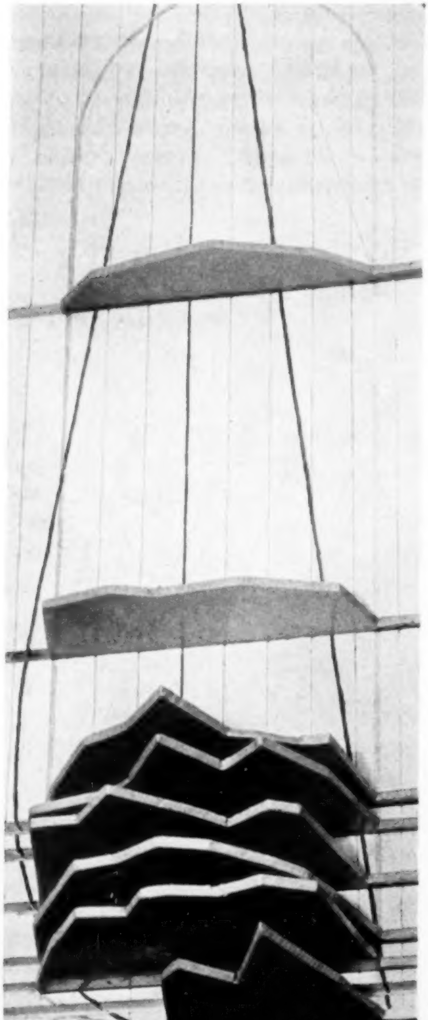

Fig. 9. Tri-dimensional Graph Showing the Rate of Growth of Root Hairs of Collards in Concentrations Ranging from 0.004 M to 0.100 M and in Different Degrees of Alkalinity and Acidity

It is to be observed that the data referred to above on the rate of elongation of root hairs in different solutions were obtained from hairs which appeared on the root ten or more hours after immersion in the solution. A consideration of the growth rate of root hairs which had been growing in air might yield somewhat different results. A limited study was made to ascertain the rate of elongation of these so-called amphibious root hairs several hours after immersion. It was found that only in solutions which support the optimum growth rate did they continue to grow during the first two hours after immersion. In all other solutions they did not grow during the first two or three hours, and then they began growing at a rate coördinate with that obtained for the aquatic hairs in the same solution. However, in especially concentrated solutions the older root hairs collapsed, those a little younger ceased growing, but did not change their form, those still younger grew after a period of rest, but changed their form or direction, while the youngest resumed growth apparently normally.

This method of studying the rate of elongation of root hairs and of plotting tri-dimensional graphs affords a means

not only of comparing one ion with another, one calcium compound with another, and one more complete solution with another, but also of comparing one kind of plant with another. Mrs. Wanda K. Farr has already begun this work. She finds that rice, with respect to its root hair elongation, exhibits a greater tolerance for acid and less tolerance for alkali

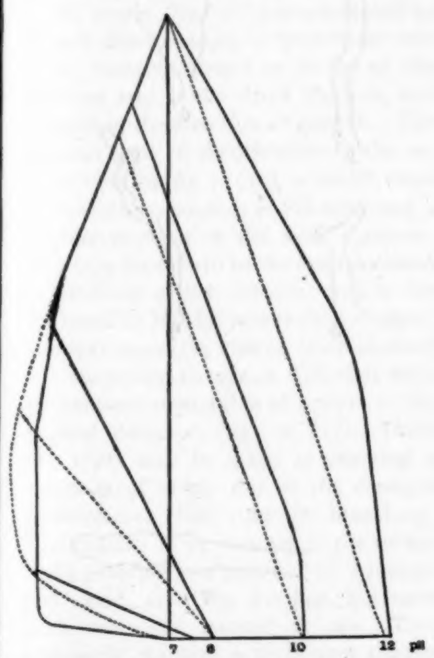

FIG. 10. CALCIUM NITRATE MAP ——— SUPERIMPOSED UPON THE CALCIUM CHLORID MAP -------

than do oats or collards. The acid limit for rice was found to be pH 2.5.

ABNORMAL FORMS OF ROOT HAIRS

The typical form for the root hairs of many plants in air and in aqueous media is cylindrical, straight, at right angles to the root, with dome-shaped tip. The root hairs of these same plants, however, growing in soil, take on many different forms, as Sachs (67) described and figured for wheat, oats, clover, and *Selaginella*. This is doubtless a response to contact with the soil particles, and to reactions to the chemicals present in the soil solution. The hairs under these conditions become enlarged at the tip, crooked, knotty, and branched. The writer (12) has found that some plants, as buckwheat, amaranth, millet, *Saponaria*, and *Gysophila*, produce root hairs which are bent, curved, or crinkled, even in aqueous media.

A number of investigators have accumulated observations as to the effect of external conditions in bringing about changes in the form of otherwise typically cylindrical hairs. Persecke was among the first to describe the various forms of root hairs. Schwarze noted a large number of peculiar forms assumed by root hairs of various plants in the presence of soil particles, in various solutions, and upon transfer to various liquid media. Wortmann (88) observed some of these forms of root hairs in sugar or potassium nitrate solutions. Reinhardt (65) noted the swelling of root hairs in these solutions and the resumption of normal form later. Sokolowa (76) has studied it very extensively, attempting to correlate the changes in form with nuclear position, lines of flow of protoplasm, oxygen content of the medium, etc. Stiehr (77) produced a number of abnormal forms of root hairs with organic compounds, such as sugars and alcohols, and with the electric current. Reference has already been made to the observation of Jeffs (36) as to the swelling of the hair in response to changes in temperature. The writer has studied the effect of calcium chloride and calcium nitrate of different hydrogen ion and molar concentrations upon the forms of aquatic and amphibious root hairs.

It has already been pointed out that very old root hairs which persist on roots have been found by McDougall (52) to have a greater diameter, with brown and thickened walls. Watson (84) has noted that on old roots of the sunflower the root hairs may branch.

A special type of abnormality of root hair growth is the so-called cap formation. It was first observed by Wortmann (88), and was later studied by Zacharias (89), Reinhardt (65), and Stiehr (77). It consists in the formation of a new wall a short distance from the tip, cutting off a short portion. In some cases Reinhardt showed several such partitions. It is usually followed by the formation of a side branch just behind the cap, which may grow out at right angles, or curve, or later resume a direction parallel to the original hair. Zacharias (89) attributed it to the plasmolysis of the protoplasm by the changed environment, while Reinhardt attributed it to cessation of growth, and resumption in a new direction. He correlated it with peculiar type of growth by Krabbe in bast cells.

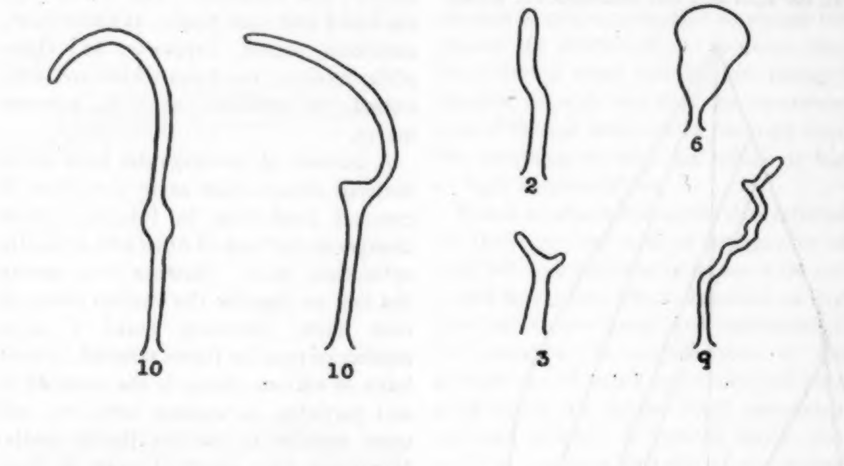

FIG. 11. TYPES OF ABNORMALITIES IN ROOT HAIRS

Stiehr (77) found a variety of changes in form upon the change of the concentration or the composition of the medium. The writer has found that these changes occur when the root is transferred from satu-

rated air to a solution, and less frequently in root hairs newly formed in the solution.

Wortmann (88) attributed these changes to alterations in turgor pressure. Sokolowa (76) considered that they are due to alterations in the oxygen pressure of the medium. It is not unlikely that more than one condition in the environment may bring them about.

The writer (fig. 11) has attempted to classify these changes in form under two types, namely changes in extent of the growing area at the tip of the hair, and changes in the direction of growth. The simplest type of modification is the so-called swollen (fig. 11 (1)), in which there is a temporary change in diameter and a later resumption of the same diameter. This type appears to be the most common in solutions of low toxicity, and is the one found by Jeffs for temperature changes. The next type is the kinked, in which there is a temporary change in direction with a subsequent resumption of growth in the original direction (fig. 11 (2)). These two types may be taken as showing a minimum of injury due to the changed environment. The next is branching. This consists in an increase in the extent of the growing area followed by a restriction again, as in the swollen, but now with two loci instead of one. This necessarily involves a permanent change in direction of at least one of the branches and usually of both and is not to be confused with the duplex hairs discussed above. Van Tieghem (82) noted such double hairs in three species of *Distichia*. Haberlandt (29) reported it about the same time, 1887, in *Brassica napus* and other cruciferae. Hill reported it in hairs growing in concentrated solutions (34), and Miss Roberts (66) figured it. The writer (19) has noted it in calcium chloride, but more commonly in calcium nitrate, where it is found in amphibious hairs and also in the aquatic hairs developing after immersion in the solution.

The flask-shaped hair (fig. 11 (4)), is not so common, but is an example of response to the shock of immersion by enlarging the areas of growth, and then a gradual recovery to normal diameter and direction. The inflated hair is by far the most common in very toxic solutions, and in the most toxic solutions which will support growth at all it is the only type found. It consists in (fig. 11 (5)) increase in diameter and continued growth at this new diameter. Hence there is no recovery to the original type. The most extreme type of abnormality, as judged on this basis, is the spatulate. It consists of growth at a progressively greater and greater diameter (fig. 11 (6)).

Next to the types of abnormalities which involve a modification followed by a return permanently to the normal, there are types of modification which display a periodicity between the new and the old. Such is for instance the beaded, in which there is an enlargement followed by (fig. 11 (7)) a return to the original diameter, then an enlargement, then a return, etc. These were not found in calcium chloride, but were not uncommon in calcium nitrate of a high pH, namely 11.0. A corresponding type, but consisting of an alteration of direction, instead of diameter, is the undulating (fig. 11 (8)), which was very much more frequent.

Perhaps the most extreme type of all is the so-called crooked, (fig. 11 (9)) in which there is a progressive enlargement or diminution of diameter, and change of direction, without any apparent rule.

The curved (fig 11 (10)) is a type in which there is a progressive change of direction.

This classification of the abnormalities of root hair form indicates that root hairs

undergo all degrees of shock and recovery. There is the temporary change with complete recovery; there is the temporary change with temporary recovery, followed by a recurrence of the new feature. There is the temporary change with a slow recovery; there is the change with slight permanent effect; there is the change with marked permanent effect. There is the change which becomes progressively more and more removed from the original type, and finally there is a complete upset of balance. Such is the response which root hairs give to changed environment; it is also the response which all living things are likely to give in a greater or less degree to sudden alteration of their surroundings, and even serves to indicate that the responses obtained in human beings to extreme conditions such as shell-shock, etc., are merely expressions of a fundamental property of protoplasm.

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CONTROLLED MATING IN HONEYBEES

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BEEKEEPING has been practiced for more than three thousand years, and more books and treatises have been written about bees than about any other farm animal, the horse and the fowl not excepted; yet practically no progress has ever been made in improving the types of these useful insects.

The great handicap to bee culture of all time is that it has never been possible to breed bees in the direction of desired varieties, as is done with cattle, sheep, poultry and all ordinary domestic animals, for the reason that the mating of the queenbee with the male takes place high in the air and free on the wing, where it cannot be controlled. She consistently chooses to manage her own nuptials to suit herself, free from human interference, instead of accepting whatever mate the beekeeper, alert for improvement of the bee population, wishes to select for her. Because the beekeeper has in the past been unable to control the male parentage of his bees, breeding for the improvement of the honeybee along scientific lines has been practically impossible.

Honeybees are not indigenous to America. It has therefore come to pass that the bees now found in this country are genetically a very heterogeneous group which has resulted from the endless crossing and intercrossing of the progeny of the numerous varieties which have been brought here, principally from the lands bordering upon the Mediterranean sea. It is true that more or less distinct varieties of honeybees exist in their own respective habitats. Thus, the native bees of Carniola, Italy, Cyprus and Caucasia constitute our most clearly defined and best known types. All of these varieties readily hybridize among themselves when the opportunity is given, and it seems certain that geographical barriers such as waters, mountains and deserts have made possible, first the evolution of these varieties, and finally their preservation through many centuries.

MATING HABITS OF HONEYBEES

The queenbee is normally fecundated by a single drone, and in the air, during her once-for-life nuptial flight. How important a part the ability to fly plays in the life of bees is intimated in the fact that queens and drones that do not possess strong, perfect wings may not hope ever to function in the perpetuation of their race.

The blind scientist, Huber, ascertained (1791) that a single mating is sufficient to fertilize all the eggs that a queen will lay in the course of two years at least, and it has later been demonstrated that this influence will last throughout the course of her whole life, which may be from three to seven years. In a few rare instances queens have been known to mate on two successive days, probably because the first mating was insufficient,

but these exceptions are so few as almost to prove the rule.

The reproductive organs of the queen-bee consist of two gigantic ovaries whose ducts, leading backwards, coalesce into a single canal, the oviduct, which hastens to its exit in the genito-anal vestibule (fig. 1). At a slight distance from the vestibule, and on the dorsal side of the oviduct, is a tiny spherical pouch opening into the latter. This is the spermatheca, the exact function of which sorely vexed the early students of insect physiology.

The gropings of the early investigators after the true explanation of how bees' eggs are fertilized, and how a queen can lay two kinds of eggs apparently at will,

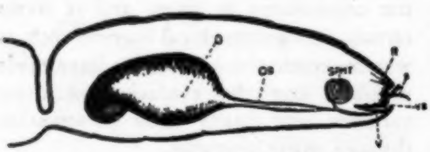

FIG. 1. FREE-HAND SKETCH OF QUEEN'S ABDOMEN

Conventionalized side view showing relative position of the reproductive organs only; *o*, left ovary; *od*, oviduct; *spmt*, spermatheca; *v*, vulva; *r*, rectum; *s*, sting; *vb*, vestibule.

constitute a long but engaging story. After years of health-breaking study, during the course of which he recorded many, but obviously not all, of the critical habits of the hive, Swammerdam concluded (1673) that queenbees were not fecundated by actual physical contact with the drones because, he said, the generative organs of the drones were quite too large. Led by the observation that when drones are shut up in a small space, as a bottle, they exhale a characteristic body odor, which he conceived to be an emanation of the "*aura seminalis*," or the *aura seminalis* itself, he concluded that in the hive this aura penetrated the body of the queen and effected fertilization. He believed that the spermatheca contained a mucilaginous secretion for sticking the eggs to the bottom of the cells.

Swedenborg believed (1750) that all the eggs of bees were unfertilized when laid, but that later the eggs in the cells were visited by the drones and fertilized individually by a contact process. Réaumur, the inventor of the thermometer which bears his name, announced (1740) that the true function of the spermatheca is to receive and hold the fertilizing material from the drone, and to deal it out, a few sperms at a time, to the eggs as they pass down the oviduct.

It remained for Dr. John Dzierzon (1845) to make his illuminating contribution, the theory of parthenogenesis, and to apply it to honeybees. This theory has never had to be changed. Substantiated by every conceivable proof, and amplified by more recent findings, the case of honeybees may now be stated as follows: all the eggs of the queenbee are unfertilized as they leave the ovaries, and they are potentially only male producing. The chorion of these unlaid eggs contains near the large end a tiny hole, the micropyle, through which a sperm may enter as the egg descends the oviduct and passes the spermathecal duct. The fusion of the sperm cell with the nucleus of an egg constitutes the fertilization of the egg, and when it hatches a female bee results. Drones have never been known to develop from fertilized eggs. But discharging eggs do not always receive a sperm as they pass the spermatheca, and such eggs are never fertilized. When hatched they can produce only drones.

The queen is the only perfect female in the hive, and her sole function is to recruit the family. The workers are also females, and are reared from the same kind of eggs, viz., fertilized eggs, but owing at least in part to the kind of food given them during the larval stage their genera-

tive organs are so dwarfed and imperfect that they cannot mate with a drone, and drones are never seen to badger worker-bees. Under certain conditions the ovaries of some workers may be developed sufficiently to enable them to lay eggs which will hatch and mature, but like those of a virgin queen, their eggs can produce only drones.

THE QUEENBEE CONTROLS THE SEX OF HER OFFSPRING

Voluntary control of the sex of the offspring is a unique gift of Nature, which is enjoyed by the queenbee. This ability is possessed by extremely few, if indeed by any other, insects, and probably for sound reasons it has never been entrusted to the hands of Man. We lack definite information as to how the queen controls the fertilization of her eggs. The feat of laying two thousand eggs a day, as she sometimes does, and of properly distributing them with almost unerring precision, the fertilized ones in worker-cells, and the unfertilized ones in the larger drone-cells, places a tremendous burden of presumption upon the discrimination of the queen.

If the fertilization of the eggs were to occur in a hit-and-miss fashion as they descend the oviduct and pass the spermatheca, then we should expect to see the queen oscillating back and forth more or less at random between the worker-comb and the drone-comb to enable her to place the eggs properly. This does not occur, and our difficulty in attempting to discredit the "will" of the queen in controlling the fertilization of her eggs is further sharpened by the classical observation that a normal queen lays eggs appropriate to the kind of comb she is on. Thus, she never seems to be obliged to leave a worker-comb for instance, and go over to a drone-comb so that she can dispose of an unfertilized egg or two before she can proceed with the laying of more fertilized eggs. The burden of precision would seem not to rest in some faculty of the queen by which she knows whether the next to be laid will be a fertilized egg or an unfertilized one; nor can it rest in any mechanics of the cell, as if its shape or size or depth were determining factors, for prolific queens sometimes follow upon the heels of the comb-builders so closely that eggs are deposited when the cells are only a third completed. Furthermore, when in the economy of the hive drones are desired, and no drone-comb is available, she does not hesitate to deposit unfertilized eggs in worker-comb. Rather does the burden of precision appear to rest in a voluntary control of the mechanism of the spermathecal duct which parcels out fertilizing material to some eggs as they pass, and not to others, depending upon the season, the condition of the colony, and the hereditary complex of the queen. Students of insect psychology are reluctant to concede voluntary acts to insects, and the concession is allowed in this case only as a makeshift till further investigations shall bring forth a more satisfactory explanation.

It has been supposed that a mated queen could continue to lay fertilized or unfertilized eggs at will just as long as there were any sperms left in the spermatheca, but this is not strictly the case. Long before the supply of sperms has been completely exhausted most queens begin to deposit a larger and larger proportion of unfertilized eggs, and as a classical symptom of approaching sterility or decrepitude in the queen these unfertilized eggs are scattered about in worker-cells.

In the phraseology of human psychology, therefore, the situation might be stated about as follows: she willed to lay

a fertilized egg, and she tried to do so, but because of the thinning out of the sperms in the fluid within the sperm reservoir, the normal draught made upon the spermatheca for fertilizing material with which to bathe the micropyle of a passing egg contained no sperms, or it contained so few that none of them found the open micropyle, and the egg got by without being fertilized. Now, having called upon her determining mechanism for a fertilized egg, she treats the resulting ovum as if it were what she ordered, and places it in a worker-cell. Thus, the presence of drone-brood scattered among worker-brood is not referable to any fault of her will, but to the exhaustion of her stock of sperms. Workerbees appear to be able to discriminate instantly between fertilized eggs and unfertilized ones, but there is no data to warrant one in attributing any such ability to queenbees.

For obvious reasons copulation in honeybees has very rarely been observed, but from the few reported observations, and more especially from the examination of queens just returning from the wedding flight we establish that the rapidly flying virgin queen is pursued by many competing consorts. The strongest drone, outflying most of his rivals, and parrying with the few, maneuvers into a position ventro-ventral with the queen. They grasp each other while still flying, the main axes of their bodies being in a position parallel to each other and usually perpendicular to the earth. In this condition copulation occurs. After normal copulation the drone is unable to extricate his organ from the vulva of the queen, and it is torn from him altogether. It is borne home by the queen and retained by her till its contents have found their way into the oviduct, after which it is dropped as a dry shred. The spermatozoa now separate themselves from the seminal fluid in the oviduct and, stimulated perhaps by chemotaxis, migrate into the spermatheca. Here they remain alive and active for months or years apparently without the taking of any nourishment, for which they have no known morphological capacity, or until they are called to leave again by the same route by which they entered.

MANY ATTEMPTS TO CONTROL MATING

The desirability of some means of controlling the mating of the queenbee has been recognized for more than a century and a half, and skilled experimenters in many lands have not ceased to attack the problem by every conceivable approach. The known attempts to accomplish this end readily fall under two general heads: (1) the isolation of the virgin queen with one or more selected drones in a limited range, and (2) forced insemination by violent or by surgical means. The following list of methods which have been tried by outstanding experimenters is by no means complete, but it is representative:

(1) Painting the vulva of the queen with fresh sperm,

(2) Queen tied out on a leash,

(3) Queen confined with selected drones in a limited range such as wire cages, small glass enclosures, immense greenhouses, on islands, and in localities uninhabited by other bees,

(4) Dropping seminal fluids into the open vulva of the queen,

(5) Queen and drone held in juxtaposition,

(6) Painting unfertilized eggs with sperm,

(7) Queen held in a block and injected.

So far as we know none of the methods catalogued above have proved to be practical for scientific or for commercial

use, except the last one, and in our own laboratory.

The artificial introduction of semen into the reproductive tract of certain of the warm blooded animals has been practiced for a long time, and the principle is scientifically sound. Prior to these investigations, however, this principle had never been successfully applied to insects. Their small size presented a baffling difficulty, but in the event that the technique could be refined sufficiently, the question still remained: does the drone merely deposit the spermatozoa within the oviduct of the queen, leaving them to make their way as best they can up the curving duct into the sperm reservoir, or does he reach farther and deliver them under compression directly into the spermatheca? The answer to this question was established by the dissection and examination of many naturally mated queens as they returned to the hive after the wedding flight.

The office of the drone in mating appears to be merely to deposit the tiny charge of semen within the oviduct of the queen. Immediately after this for the next four to seven hours, and stimulated by some force which is not fully understood, the individual spermatozoa, numbering perhaps a million or more, set up a powerful lashing of their flagella by means of which they work their way up the duct, and collect at last in the spermatheca.

A critically important item relating to the physiology of copulation in honeybees should be mentioned here. Queens freshly mated, as they return to the hive, are observed always to bear in the genito-anal vestibule a copious mass of mucus from the accessory mucous glands of the male. The function of this mucus is to harden in contact with the air, and be a sort of plug to close the vulva, preventing the back flow of the semen, and protecting it from exposure to the air. It has been established by repeated experiments that if the mucous plug is torn away from a normally mated queen, or even slightly meddled with before she has borne it for two or three hours, she may be temporarily or permanently incapacitated to lay fertile eggs.

THE APPARATUS

The insemination of a queenbee is by nature a microscopic operation, and a binocular microscope giving a magnification of 15 to 18 diameters is indispensible. An all-glass syringe convenient for handling the tiny bead of semen from a single drone seems not to be made commercially anywhere, and we are compelled to design and construct our own. The critical specifications of this syringe are (1) a straight, all-glass plunger barrel of perfectly uniform bore 0.5 millimeter in inside diameter, and (2) a tight fitting plunger controlled by a fine-threaded screw allowing a plunger stroke of 15 to 20 millimeters.

A consideration of first magnitude in this work is that every movement shall be under perfect control. To control and stabilize the movements of the micro-syringe, this instrument is clamped in the jaws of a Barber pipette-holder (fig. 2). The turning of one or another of the three nurled screwheads set at right angles to each other in the three planes of space slowly moves the syringe forwards and backwards, up and down, right and left. This micromanipulator is mounted on a flange which rises from a false stage fitted over the real stage of the microscope, and is tilted so as to incline the syringe at an angle of about 40 degrees to the horizontal, thus permitting the operator to look into the vestibule of the queen while emplacing the syringe.

The queen also must be securely held

perfectly motionless to prevent her from injuring herself by struggling. With careful handling she is placed dorsal side downward in a form carved out of a small block of wood (fig. 3) just to fit her thorax, head and abdomen, with the tip of the abdomen extending slightly over the edge of the wood. Furthermore, this little operating-table tilts her up so that the long axis of her body is in direct line with the long axis of the microsyringe. She is held motionless in this position by several strands of silk thread thrown over her body and around the operating-table. Much caution is needed to insure that her wings and legs are in comfortable position, for if she should emerge from the ordeal with twisted legs or crumpled wings she would not be acceptable to the bees.

A strong, steady light is needful to facilitate work on dull days and at night, but it is unwise to let strong artificial light shine directly upon the queen, or upon the spermatozoa. We employ a shaft of parallel light from a 150-watt microscope lamp, reflected and focused by a concave mirror, but we do not expose her to this intense light for long at a time.

THE TECHNIQUE

A few minutes before tying the queen down we liberate a few choice drones on the inside of the window. The strongest ones demonstrate their strength by flying hardest and longest against the pane, while the weak and immature ones settle down soon to rest at the bottom of the window. While this assorting of the drones is in progress we lightly seize the virgin queen to be injected, make her fast in the form on the operating-table, and set her aside to wait while we fill the syringe. If she has been out of the hive very many minutes she is hungry, and she will probably accept a taste of thin honey given to her on a toothpick as she waits.

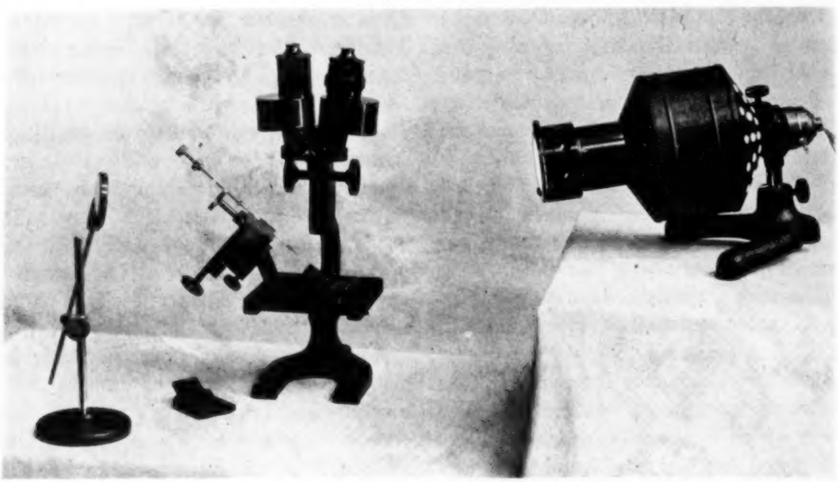

Fig. 2. Showing the Position of the Apparatus Ready for Work

From the few drones still flying on the window we seize one of the most vigorous fellows, and clip off his head. The shock of decapitation will probably cause him to evert the copulatory organ more or less

completely. Sometimes merely seizing a drone, or lightly twirling him in the fingers will cause him to react in this way. If decapitation does not cause him to ejaculate he is discarded, and another one is tried. When the desired reaction

FIG. 3. THE OPERATING-TABLE, NATURAL SIZE
The cradle exactly fits the head, thorax and abdomen of the queen

is obtained (fig. 4), we grasp the everted curved organ with sharp tweezers and pull it loose from the body. With the penis is brought away also the so-called bulb or seminal pouch swollen with its

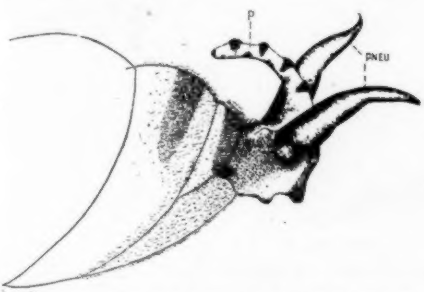

FIG. 4. SHOWING THE GENITALS OF THE DRONE AS THEY APPEAR AT THE MOMENT OF EJACULATION
P, penis; *pneu*, pneumophyses

tiny charge of creamy colored sperm and pearly white mucus (fig. 5).

With sharp scissors we snip off the ejaculatory duct at the point where it begins to widen to form the bulb, quickly lay the detached bulb on the index finger of the left hand, and pass it into the magnified field of the binocular. The separate regions of the mucus and of the sperm are now easily distinguished by their colors, and the degree of magnification suggested above readily permits the operator to observe the swirling masses of spermatozoa through the thin walls of the bulb.

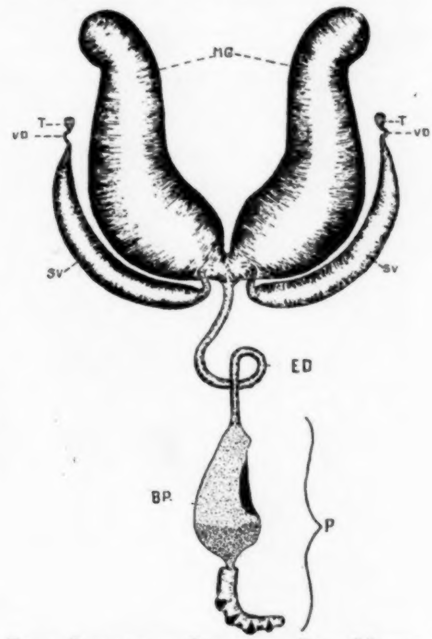

FIG. 5. REPRODUCTIVE ORGANS OF A FULLY MATURE DRONE, PARTIALLY CONVENTIONALIZED
Showing relative position after ejaculation has been induced and the organs have been pulled away with the tweezers. *Mg*, accessory mucous glands; *sv*, seminal vesicles; *vd*, vas deferens; *t*, testicle; *ed*, ejaculatory duct; *p*, penis; *bp*, bulb of the penis. Note that the pneumophyses are left behind with the abdomen. The regions of the sperm and of the mucus in the bulb, *bp*, are clearly visible.

The finger is now moved forward so that the tip of the syringe is made to enter the region of the white mucus through the opening where the ejaculatory duct was cut off. The plunger is screwed back about two millimeters, thus taking up a little of the mucus. The finger is then advanced slightly so as to bring the point

of the syringe into the midst of the yellow sperm. This is about all taken up, leaving the collapsed bulb nearly empty. The virgin queen still resting on the operating-table, and having been fed, is now brought into the magnified field, and placed with the tip of the abdomen in the center of the field, and pointing toward the syringe. The operating-table is made vered into such position that when allowed to open slightly they push back the plates, and expose to view the sting, sting palps, rectum and vulva. While the left hand holds the vestibule open (fig. 6) with the tweezers, the right hand operates the controls of the micromanipulator so that the tip of the syringe stands just over the opening of the oviduct,

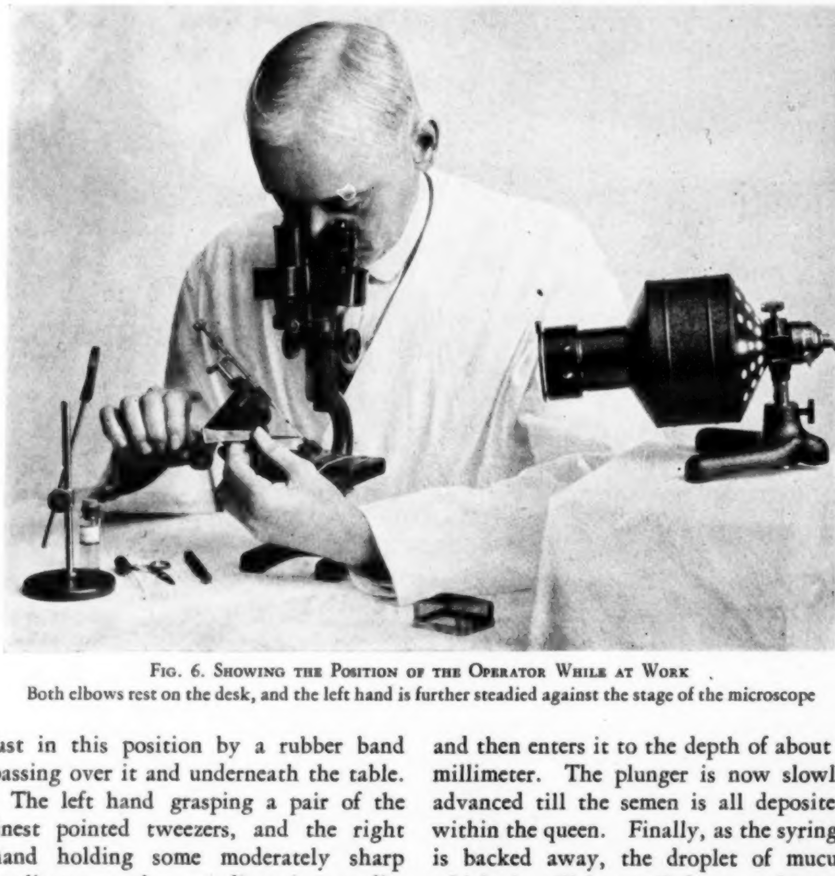

Fig. 6. Showing the Position of the Operator While at Work

Both elbows rest on the desk, and the left hand is further steadied against the stage of the microscope

fast in this position by a rubber band passing over it and underneath the table.

The left hand grasping a pair of the finest pointed tweezers, and the right hand holding some moderately sharp applicator, such as a dissecting needle, now coöperate to pry apart the genito-anal plates of the queen, an operation which some queens resist with remarkable force. The tweezers are gently maneu- and then enters it to the depth of about a millimeter. The plunger is now slowly advanced till the semen is all deposited within the queen. Finally, as the syringe is backed away, the droplet of mucus which, it will be recalled, was taken up ahead of the semen in loading, is the last to be discharged, and is left to thicken in and over the vulva as a plug to prevent any back flow and to shut out the air.

The queen may now be released from the operating-table, both wings on one side clipped off to prevent any subsequent flight in pursuit of further nuptials, and then returned to her own bees. If she received no injuries during the operation she will be accepted by her own bees with the same etiquette as if she were only returning from a natural wedding flight. If all is well she will begin oviposition in a day or two, and follow in every respect thereafter the rôle of a normally mated queen.

Instrumental insemination of queenbees is in its infancy. Its first birthday has just passed. Successful queens began to appear in the autumn of 1926. Because of the lateness of the season it was not possible to culture many of the treated queens through a complete life cycle before winter. Data as to the success or failure of the operation, therefore, were gathered from about 40 of the treated queens by determining the presence or absence of spermatozoa in the spermatheca under dissection. Somewhat more than 50 per cent of the queens examined were found to have received insemination ranging all the way from very slight up to normal.

MATURE DRONES NECESSARY FOR SUCCESS

Let it be recalled that the spermatheca of a virgin queen contains only a thin, clear liquid, but that after successful insemination, either natural or instrumental, this liquid appears thick and opaque because of the million or more of spermatozoa suspended in it. The mating of a normal queen with a vigorous drone results in the dense crowding of the sperm reservoir with motile sperms, but if the mating occurs with a less vigorous male the number of sperms received may be very much less, and her period of usefulness as a layer would obviously be proportionately shorter. To enable her to head a populous colony successfully for the usual span of two or three years, it is necessary that the queen should have the most copious insemination possible in the beginning, because (1) queens do not take mating flights on successive years to replenish their stock of sperms, and (2) there is no multiplication of sperms within the spermatheca.

Whether a queen that has received scant insemination, either on the wing or under the microscope, will attempt to make subsequent flights in pursuit of further nuptials seems not to be governed by any regularity which we now understand. Some queens that have received insemination equal only to about 5 per cent of the normal degree never show any desire to mate again, but turn themselves at once to a rapid but brief period of egg laying; other queens that have received as much as 50 per cent of the normal amount of insemination never lose the passion to get out on the wing and mate again.

BETTER EQUIPMENT NEEDED

The second season of instrumental insemination has seen no great changes in the equipment used nor in the method of using it. Some improvement in technique is suggested by the fact that the proportion of queens receiving some degree of insemination has risen from 50 per cent in 1926 to 65 per cent in 1927. The need has been felt for a more convenient and more adaptable form of operating-table, and designs are incubating for a perfectly stabilized retracting device to hold open the genito-anal vestibule of the queen while the syringe is being emplaced. Especially is it to be desired to have this function performed under better control than is possible by the pulsating left hand of the operator.

PRESENTATION OF DATA

Brief inspection of the following data taken from the records of 1927 serves to show how subtle are some of the factors dealt with in the problem of controlled mating of these insects. In all 96 virgin queens were treated from once to ten times each depending upon their behavior. To prevent their leaving the hive at any time in pursuit of natural mating the hive entrances were always closed with perforated zinc which allows workers to pass in and out freely, but will not allow queens and drones to pass. If a treated queen was seen trying to leave the hive she was taken to the laboratory and treated again. Thus, some queens were fully inseminated as the result of one injection, and one queen is known to have received only 50 per cent normal insemination after nine injections. To ascertain at once the extent of insemination the spermatheca was dissected out and crushed under a microscopic cover slide. The degree of insemination was then estimated in per cent of the normal.

Of the 96 queens that were treated 66 per cent received an appreciable degree of insemination and 34 per cent received no sperms into the spermatheca. Furthermore, of all the queens that received an appreciable degree of insemination,

79% received 5% normal insemination or more
38% received 10% normal insemination or more
17% received 50% normal insemination or more
11% received 75% normal insemination or more
6% received 100% normal insemination

During the course of the season several promising queens disappeared for one cause or another before any brood was produced, and there was no means of determining whether they would have been successes or not. In making the records such missing queens were counted as total failures although probably some of them were inseminated.

To estimate the degree of insemination of queens that are still living, note was taken of the percentage of worker-brood produced by them. For example, if 10 per cent of her brood was sealed flat by the workerbees, and the rest was sealed oval, a queen was estimated to have received about 10 per cent of the normal degree of insemination. The absence of any oval, or drone-brood, was taken to mean that her insemination was normal. This method of arriving at the results of treatments is obviously open to criticism. However, during the first few weeks of her life as a laying queen, and especially when a treated queen is being cultured in a nucleus, there has been found to be a remarkably close correlation between the degree of her insemination and the proportion of fertilized eggs that she lays.

WHY ARE RESULTS SO VARIABLE?

That instrumental insemination of queen-bees is still in the experimental stage is evidenced by the large proportion of queens that receive only partial insemination as the result of a single injection. It still frequently happens that when half a dozen queens from the same hatch are treated exactly alike on the same day, some will be copiously inseminated while others are complete failures. Repeated injections build up the degree of insemination, but repeated injections are impractical in most hereditary studies. Queens that have received less than 10 per cent normal insemination cannot be depended upon to settle themselves to oviposition; however, as low as 5 per cent of worker-brood may be quite sufficient to enable valuable genetical studies to be made. To the question, why are the results so variable, we are compelled in candor to answer that we do not yet know.

In systematic search for an underlying cause of such wide differences in results, both the technique and the general condi-

tions of the experiment have been varied within wide limits. The size of the dose of seminal fluids injected has been varied; some queens have been injected rapidly, and others very slowly; the exposure of the seminal fluids to sunlight, to artificial light, and to heat and cold has been widely varied; some queens have been injected when only seven days old, while others were allowed to attain the age of fifty days before being treated; with some queens the dose consisted of nearly pure sperm with almost no admixture of mucus, with others of a loose mixture of sperms and mucus; sometimes the dose was made to consist of a suspension of semen in normal physiological saline solution, and sometimes of a mixture of semen from several drones all at once. So far these variations of procedure have not led to the uncovering of any certain cue, in either a positive or a negative way.

DRONES SUSPECTED OF INFERTILITY

The condition of the problem at the present time casts a glance of suspicion toward the drone. A fund of evidence has accumulated which lightly points to the possibility that partial or complete sterility of the drones may be the variable factor; that motility of the sperms is not a dependable criterion by which to judge of their functional maturity. More and more we find ourselves selecting for laboratory use the oldest drones obtainable. Furthermore, there is little evidence to warrant the assumption that all the drones that ejaculate when decapitated are functionally mature. When we can have them, we prefer drones that ejaculate vigorously when merely seized and gently twirled between the thumb and fingers. Every beginning is a struggle against inertia, but a beginning has been effected, and the problem bristles with genetical and economic possibilities.

OTHER SCIENTISTS SUCCESSFULLY REPEAT THE EXPERIMENT

Developments to the present time confirm the belief that the principle of instrumental insemination is practical as a means of controlling the mating of honeybees. The trend of the technique is in the direction of greater simplicity, the actual operation being somewhat simpler now than was at first thought possible. Several experimenters after witnessing a few demonstrations have been able to take the equipment and inseminate queens for themselves. This fact must not be interpreted to mean that instrumental insemination in its present development is adapted to the immediate use of workers untrained in microscopic technique. In the hands of a microscopist, however, the operation is very simple.

HONEYBEES PROMISE TO BE VALUABLE MATERIAL FOR GENETIC RESEARCH

Perfect control of mating in honeybees places the new science of honeybee eugenics in the biological curriculum. An attractively large number of the qualities necessary for ideal material upon which to make genetical researches are present in honeybees. The following may be mentioned: (1) The life cycle is short; three or more generations may be reared in one season. (2) A single mating gives a large amount of progeny. (3) Bees are large enough to permit much scrutiny without the use of microscopes. (4) The present known measurable hereditary characters of bees are not very numerous, yet there is reason to expect that many more such characters will be discovered when bees are more carefully scrutinized. (5) Bees are hardy; they are easily cultured, and due to their agricultural relationships, any race betterment achieved

with them would have immediate economic value. (6) Finally, the fact that all the eggs of honeybees are potentially parthenogenetic after maturation should serve to simplify certain genetical methods.

The first task in attacking a problem in genetical analysis is to determine whether the parent stocks which are to be used are homozygous for the characters to be studied. Nearly all of the breeding experiments so far performed have, therefore, been directed toward this end. Let it be reiterated that American honeybees are extremely heterozygous. A task of considerable dimensions looms ahead of segregating and stabilizing pure strains of the types we design to work with. The pursuit of this problem during the past season was made possible by the award of an August Heckscher Research Assistantship under Dr. R. A. Emerson in the Plant Breeding Department at Cornell University. A beginning has been made with five of the best defined varieties of bees as follows: golden Italian, Carniolan, Caucasian, Black (German) and so-called Albino.

ONE QUEEN INSEMINATED FROM ANOTHER QUEEN

The mention here may be appropriate of a new experiment which was performed during the past season. This consisted in inseminating a virgin queen with sperm dissected from the spermatheca of a mated queen. Number 38 was a black virgin queen who on her twenty-fourth day was injected with sperm taken from the sperm reservoir of a golden queen who had been mated on the wing some weeks before, and who appeared normal in every way, but who never laid well. Two days later number 38 was dissected and found to have received a slight but certain degree of insemination. This experiment admittedly partakes of the nature of a laboratory curiosity, but the pure science of today sometimes becomes applied science tomorrow.

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EXPERIMENTS ON LONGEVITY

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(The substance of this paper was presented as a lecture, on the Schiff Foundation at Cornell University, May 9, 1928)

THE PROBLEM

THERE is something fascinating in the idea of experimenting with longevity. The span of life is a rude and uncompromising inhibitor and limiter in human affairs. Just about the time that a man's experience in living has attained a sufficient magnitude to give him some confidence that he has acquired a little skill in that difficult art, Death comes stalking along and ends it all. Furthermore death, coldly and unfiguratively considered merely as a biological process, has the unfortunate characteristic of irreversibility. So any experimental approach to its study, with man in the traditional guinea-pig rôle, is not feasible.

In the face of such a situation there are two things which the person curious about death, longevity, and similar subjects may do. He may either content himself with the monotonous *pabulum* of human vital statistics—not entirely innutritious, to be sure, but still a diet so narrowly constructed, so lacking in savor, and so full of indigestible residues that it has a tendency to induce in those who nourish themselves exclusively upon it a certain bilious and acidulous temperament, a leptosomal *habitus* of body, and mental delusions of righteous exactitude as irritating as they are unwarranted.

Or, on the other hand, the inquisitive person whose dilemma we are endeavoring to resolve, may study mortality and longevity experimentally, in some organism other than man. This means that he can subject his animals to all sorts of influences, completely under his control, and see how their duration of life is affected. Out of all this are likely to come many thrillingly unexpected things. On account of the general happiness and good cheer thus engendered there is induced a tendency towards a pyknic or eurysomal *habitus* of body, and a tolerant realization of the liability of human beings to draw erroneous conclusions from what seem—but unfortunately too often *only* seem—to be plain facts of nature. There is sound tradition for such an effect. The Greeks, the Chinese, and the Hindus all represented their gods as of a pyknic habit, and, as everyone knows, the chief activity of gods is to make biological experiments with human beings.

Not wishing to miss any of the pleasures of life, I have myself tried both the statistical and the experimental methods of studying mortality and longevity. But tonight I shall speak to you only about the results reached by the latter method. In short our discourse is to be about such lowly organisms as flies and muskmelons, and has nothing whatever to do with man directly. Perhaps the

general biological principles which we shall find operating in these lower forms relative to longevity also apply, in some degree, to the determination of the human life span, but I am not prepared positively to assert that this is so in this particular case. There seems to me to be some humanity, it is subject to the same laws as those which govern the animals from which it has arisen."

LIFE TABLES

The simplest experiment that can be performed about longevity is to take a

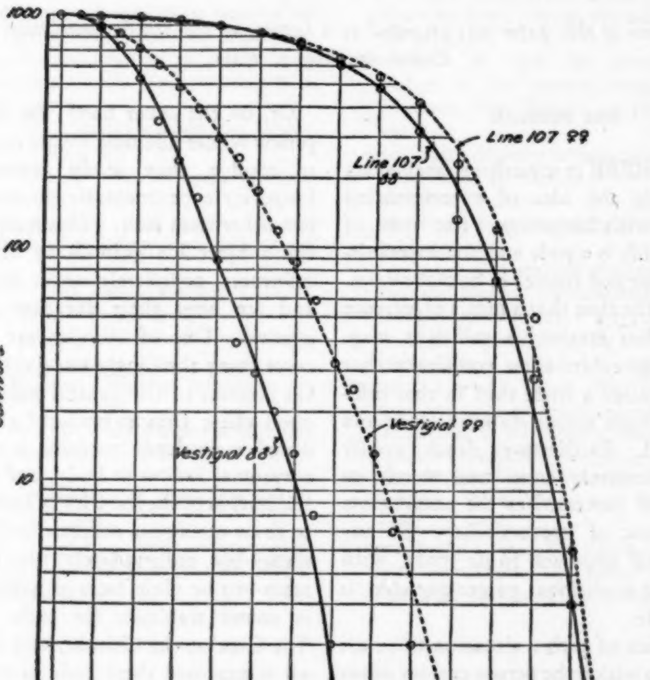

FIG. 1. SHOWING THE NUMBER OF FRUIT FLIES SURVIVING AT DIFFERENT AGES, OUT OF 1000 STARTING IMAGINAL LIFE TOGETHER

The upper pair of lines relate to the normal wild type *Drosophila*, and the lower pair to the mutant *vestigial*

probability that it is so, but how great this probability is cannot be precisely evaluated in the present state of knowledge. I have confidence, however, in the general biological principle recently stated by J. B. S. Haldane in these words: "Whatever additional facts may be true of considerable number of individual organisms, say a thousand fruit flies (*Drosophila*), at the moment of birth (which we shall for convenience in the case of *Drosophila* take as the moment of emergence as imago from the pupa case), confine them in suitable receptacles for

observation, feed and care for them properly, and observe the times at which the individuals die, until the last one of the thousand has ceased to live.

The result of such an experiment is shown in figure 1.

These curves bring out several important points regarding the duration of life in flies. The first is that there are differences between individuals in respect of longevity. Under identical conditions of environment, housing, feeding, etc., some individuals live longer than others, and the distribution of these differences in longevity is a regular and characteristic one. In the second place, if we compare the upper two lines of the diagram, which depict the facts for normal, wild type *Drosophila*, with the lower two lines, which relate to the mutant form vestigial, characterized by greatly reduced and distorted wings, it is seen that these two different races or strains of flies have, as races, characteristically different average durations of life and different distributions of longevity under standard laboratory conditions. Vestigial flies live, under the same environmental conditions, only about a third as long as normal wild type flies, on the average. Finally the diagram shows that female flies live longer than males, on the average.

The facts shown in figure 1 are descriptive of the distribution of longevity in populations of flies of two sorts, wild and vestigial. But, like all descriptions of natural phenomena, their primary effect on the inquiring mind is that they definitely formulate problems. What we want to know is why it is that some individual flies live longer than others, and that some kinds of flies (normal wilds) live longer than other kinds (vestigials). When we say "why" in this connection, what we really mean, of course, is that we want to know what are the variables which are causally determinative of the observed facts. Let us now see what can be found out in this direction.

INHERITANCE OF LIFE DURATION

The first question which occurs to the biologist when confronted with any such problem is naturally as to what heredity has to do with the results. Light upon this query may be got in two different ways. We may first try to determine whether differences in longevity between individuals of the same strain and in the same population have a genetic basis.

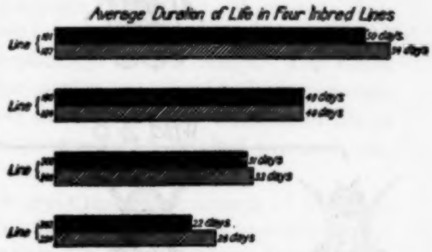

FIG. 2. SHOWING THE MEAN DURATION OF LIFE, IN DAYS, OF FOUR INBRED LINES OF DROSOPHILA, ALL ISOLATED ORIGINALLY FROM THE SAME GENERAL POPULATION

The solid bars show the duration of life in the line at its first test, and the cross-hatched bars the duration of life in the same line tested about seven months later.

One way of doing this, which is standard in genetic methodology, is to form inbred lines through the process of successive brother × sister matings, and then see whether significant differences in longevity are permanently characteristic of different inbred lines so produced. The result of such experiments on duration of life in *Drosophila* is to show that, in fact, inbred lines or strains showing permanent differences in longevity can be produced by isolating and propagating in this way individuals from a general mixed population which, in current genetic terminology, is not homozygous relative to the

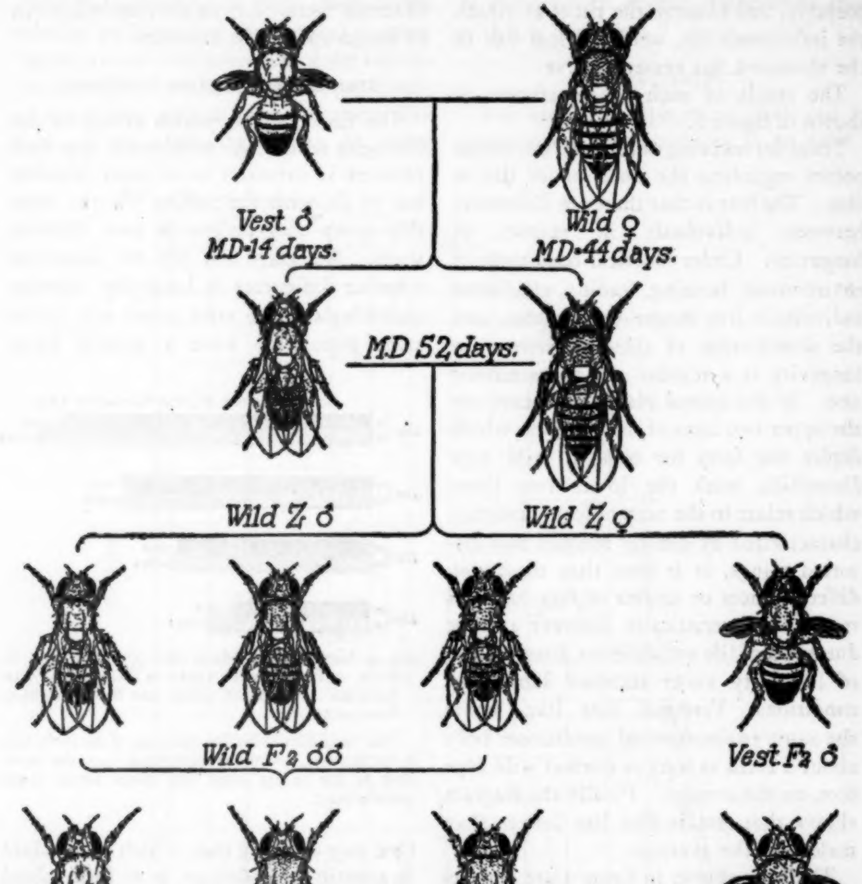

Fig. 3. Pedigree Diagram Showing the Results in the First Two Generations of Crossing a Vestigial Mutant with a Normal Wild Drosophila

genetic factors which may be presumed to determine longevity. Examples of this are shown in figure 2.

This diagram demonstrates conclusively that there exist in a general population of *Drosophila* large differences in longevity which can be made permanent by breeding. As a matter of fact some of these lines are still carried as stocks in the laboratory, and have preserved substantially unchanged the average duration of life shown in figure 2 for eight years, without further selection, or brother × sister mating.

Another kind of evidence demonstrating the inheritance of longevity in *Drosophila*, under constant and defined environmental conditions, can be obtained by crossing a long-lived strain with a short-lived strain, and analyzing the results in successive generations of progeny in the usual Mendelian manner. Such crosses were first made between normal wild type flies and the mutant vestigial. Figure 1 shows that these two kinds of flies have markedly different average durations of life and different life curves.

The chief, broad results of such a crossing experiment are shown in figure 3.

When flies carrying the mutation vestigial are crossed with normal, wild type flies, the wing mutant character vestigial behaves as a simple Mendelian recessive, without sex-linkage, since the gene for vestigial is located in the second chromosome. The first generation flies from such a cross are all of the normal wild type, with normal wings. When these first generation flies are mated with each other, they produce a second generation in which individuals bearing normal wings and individuals bearing vestigial wings occur in the theoretical proportion of three of the former to one of the latter. The actually realized proportions approximate to this theoretical ratio.

In respect of duration of life the facts are these. The vestigial strain used as parent in the cross had an average duration of life of approximately 14 days. The wild type strain used as the other parent had an average longevity of 44 days. In the first generation flies, which are all of normal wild type morphologically, the mean duration of life was approximately 52 days. When these first generation flies were bred with each other the wild type flies of the second generation had a mean duration of life of 46 days, while the recessive vestigial flies of this second generation had a mean duration of life of only 13 days. There thus appears a clean segregation in respect of average longevity exactly paralleling that in the morphology of the wings. The forms segregated in the second hybrid generation have the same average duration of life as the corresponding original parent forms, to within one or two days.

A great many experiments of this type have been carried out in my laboratory, involving a number of mutations other than vestigial. What they all show clearly is that duration of life behaves like a segregating character in the Mendelian sense. How are these facts to be interpreted?

The most reasonable interpretation, consonant with all the facts, seems to be to assume that duration of life, considered of itself, is not a biologically separate characteristic of the organism, but instead is simply the expression of the total functional-structural organization or pattern of the individual. It is apparently this organization or pattern which is inherited, and not duration of life as such. Duration of life is only one of many objective manifestations of the thing which is inherited. Put in another way, what this view of the matter says is that if the duration of an individual's life is an implicit function of the individual's or-

ganization or constitution (presumably a purely physical and chemical thing fundamentally) and if constitution or organization is inherited, it follows that duration of life will behave exactly as though it were itself inherited.

In the experiments here described it would seem that the gene for vestigial, besides affecting the form, size and behavior of the wings of *Drosophila*, *also* influences in and through its effects on the total organization pattern of every fly in which it is present, the duration of life of that fly. We have measured with considerable exactness and manifoldness what the quantitative effect of this gene is upon duration of life (and, of course, at the same time the effect of its allelomorph, the gene for normal wing), under standard and constant laboratory conditions of feeding, etc.

The view of the case which has been sketched seems to be in accord with the best current opinion as to the biological meaning and effect of mutant genes generally.

DENSITY OF POPULATION AND LONGEVITY

Shall we regard the matter as now settled, and conclude that in the genetic constitution of the individual we have the determining cause of its longevity? Before doing so it would seem the part of wisdom to see what effect environmental changes may have upon the duration of life of *Drosophila*. We have made many studies in this direction, but within the present time limitations it will be possible to discuss only one environmental factor. This one is the density of population in the universe wherein the individual lives its life; or, to put the case in less technical terminology, the degree of crowding to which the individual fly is subjected by its fellows.

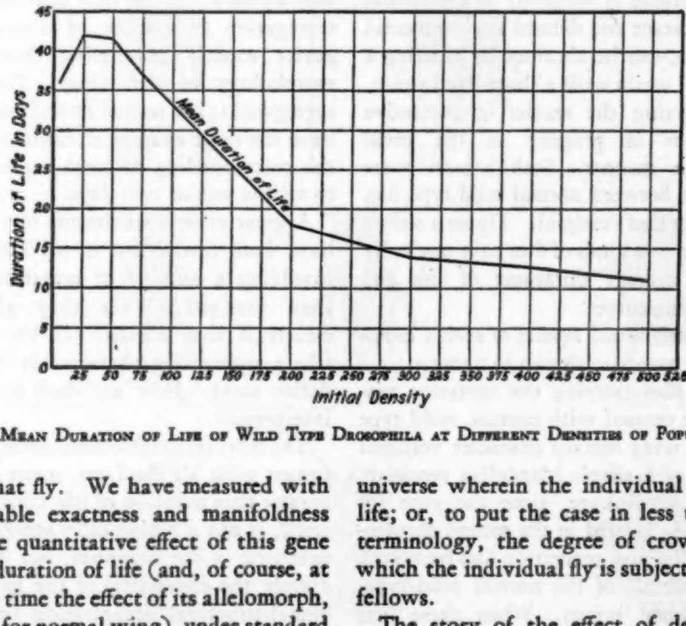

FIG. 4. MEAN DURATION OF LIFE OF WILD TYPE DROSOPHILA AT DIFFERENT DENSITIES OF POPULATION

The story of the effect of density of population upon longevity is such a long and complicated one that it will be impossible here to do more than touch briefly upon its high points. If one makes up a series of one-ounce vials each containing newly hatched flies, in numbers varying from one or two pairs per bottle

up to say 500 flies, and then determines the time of death of each fly in each bottle, it is found that the average duration of life follows, with increasing density, the course shown in figure 4.

Between initial densities of 2 and 15 flies per ounce bottle the mean duration of life increases rapidly with increased density. Between densities of 15 and 55 flies per bottle there is a slow and gradual increase in average longevity. In fact it is not certain that this region of the curve does not really represent a plateau of optimal density, in which region small differences in density have no great effect upon average duration of life. After a density of 55 flies per bottle is passed longevity declines steadily with advancing density.

The form of the upper limb of the curve of decreasing average longevity with increasing density of population suggests that there is a tendency to approach a constant level at extremely high densities. There is only a very gradual decline of mean duration of life with increasing densities of population after a density of 200 flies per bottle has been passed. Beyond this density little further effect on longevity is produced by greater crowding.

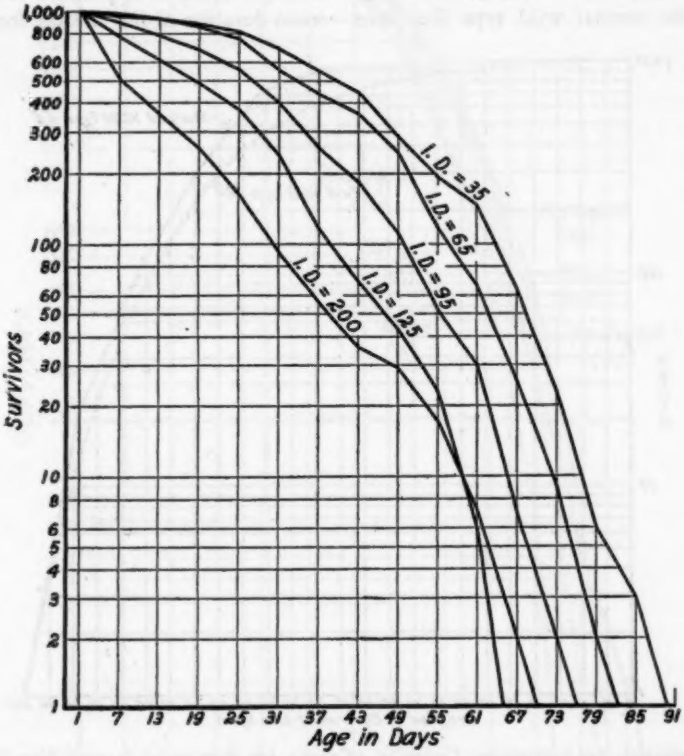

FIG. 5. SURVIVORSHIP DISTRIBUTIONS FOR INITIAL DENSITIES OF 35, 65, 95, 125, AND 200 WILD TYPE FLIES PER BOTTLE

If we examine the curves of survivorship at different densities of population certain further points of importance are apparent. In figure 5 are shown survivorship curves at the optimal density of 35 flies per bottle, and at five higher densities.

From figure 5 it is seen that at density 200, not only has the mean duration of life of the normal wild type flies been greatly reduced, but also the survivorship curve for such flies has been transformed into something practically identical with the straight line diagonal type of life curve shown in figure 1 to be characteristic of the mutant fly vestigial.

So then we find ourselves in a somewhat paradoxical situation. One body of experimental evidence seems to show clearly that differences in life duration and in the form of the life curve have their foundation in the genetic constitutions of the individuals—in heredity, in short—whereas another body of equally careful and cogent evidence indicates that by appropriate modification of the environment (density of population) it is possible to alter the mean duration of life and the form of the life curve of long-lived wild type *Drosophila* to a point where these characteristics become substantially identical with those normally found in the short-lived mutant form vestigial.

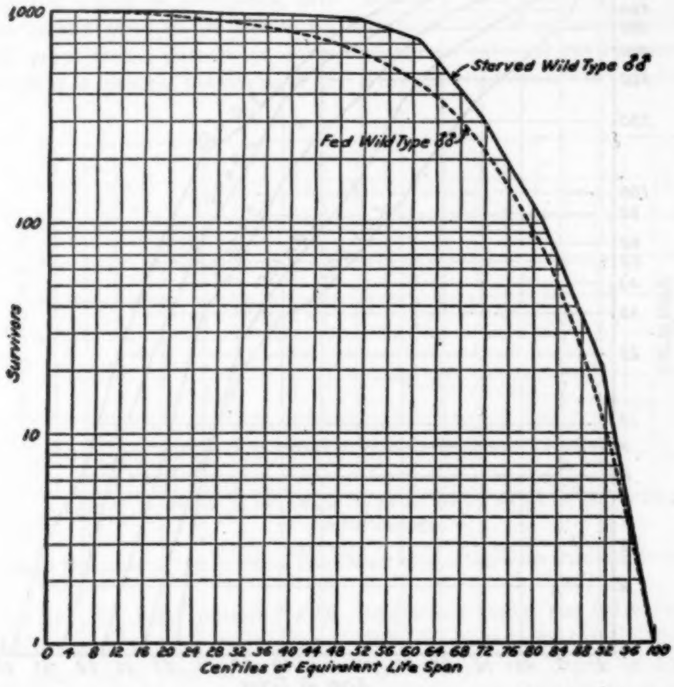

FIG. 6. COMPARING THE SURVIVORSHIP CURVES IN A CENTILE AGE BASIS OF (*a*) STARVED WILD TYPE MALES (SOLID LINE) AND (*b*) FED WILD TYPE MALES (BROKEN LINE)

Plainly further, and more penetrating, analysis of the situation is demanded. In order to accomplish this attention may next be turned to a different line of experi-

mental approach. Experiments were carried out, with the most painstaking attention to details of technique, in order to secure reliability of results, in which flies were hatched under such conditions that, fed flies. Two general results of significance emerged from these experiments. The first is shown in figure 6, and the second in figure 7.

In making this diagram, shown in

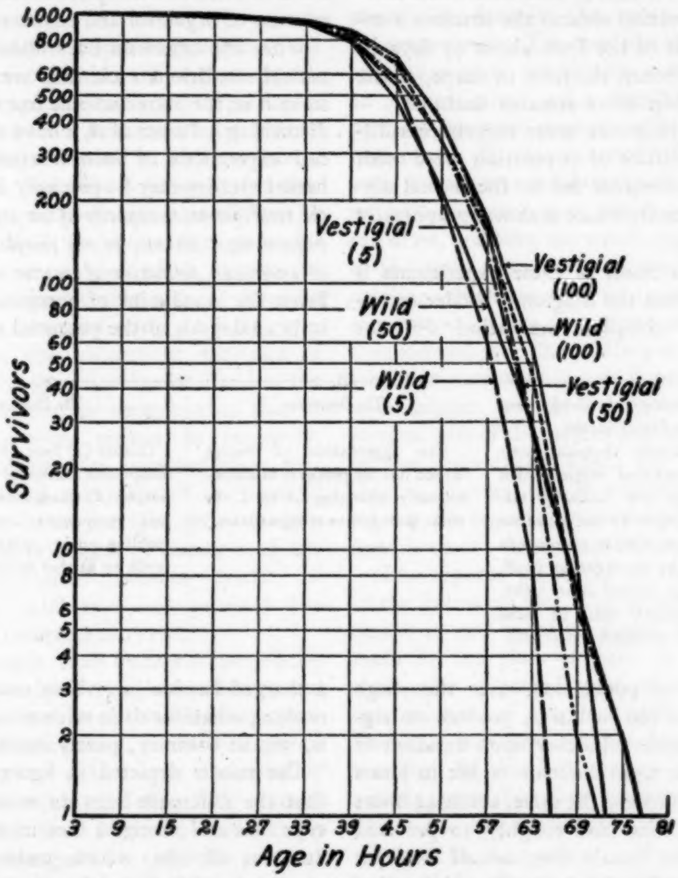

Fig. 7. Survivorship Distribution for Normal Wild Type and Vestigial Drosophila, under Complete Starvation at Three Densities of Population

as fully developed flies, they could never obtain any food. Under the conditions of complete starvation the durations of life of large numbers of individuals were observed. These durations were a matter of hours, instead of days as in the normally figure 6, it was necessary, in order to compare the forms of the life curves of fed and starved flies, to measure age in relative terms, instead of absolutely in hours or days. This was done by taking the total life span as 100 per cent of life duration,

in the case of both fed and starved flies. Then age may be expressed in both cases as hundredths, or centiles, of their own life span in the case of each group of flies. When this is done, with the result shown in figure 6, it is seen at once that while complete starvation reduces the absolute average length of life from about 45 days to about 45 hours, the *form*, or shape, of the survivorship curve remains *unaltered*.

In carrying out these experiments different densities of population were used. This circumstance led to the second significant result, which is shown graphically in figure 7.

The net result of these experiments is evident from the diagram. Under conditions of complete starvation different densities of population, over the range from 5 to 100 inclusive, produce no significant effect whatever upon duration of life. The mean duration of life in hours is approximately the same, about 44 hours for male flies, and roughly 10 per cent higher for female flies, *at all densities*, and for both wild type and vestigial flies.

INHERENT VITALITY

From the point of view of theoretical biology the condition of complete starvation is an interesting one. It means that we are observing the physiological behavior of the organism in pure form, so to speak. This is evident from the following adaptation of Cuvier's old "whirlpool" conception of the organism.

A ⟶	B ⟶	C
External Sources of Energy and Non-Living Matter	*The Organism*	*The Product*
(Food. Either chemical compounds of external origin which yield energy and utilizable material when split by the organism (animals), or similar compounds synthesized by the organism itself, with energy derived from light, and subsequently split to yield energy and utilizable material.)	(An aggregation of matter which has the property of autonomously changing A to C, *by virtue of its pattern or organization*.)	(Either (*a*) heat, (*b*) work, (*c*) component matter of the organism, or (*d*) waste, meaning chemical compounds incapable of yielding energy with economic profit by further splitting.)

The concept of the organism embodied in this scheme is, of course, an old one. Lately Pikler has discussed a similar but more detailed and complete outline of the relation of organism and environment.

What the organism does under experimental conditions such that we can observe B of the above scheme free from the disturbing influence of A, I have chosen to call expressions of *inherent vitality*. Inherent vitality may be precisely defined as ***the total potential capacity of an organism to perform vital actions, in the complete absence of exogenous derivation of matter or energy.*** From the standpoint of energetics solely it is analogous to the potential energy of a charged Leyden jar. This concept has nothing whatever to do with vitalism, but is, on the contrary, purely mechanistic.

The results depicted in figure 7 show that the difference between normal wild type flies and vestigial flies in respect of duration of life, which under normal conditions of feeding (that is, when it is the expression of the total vitality implicit in the normal $A + B$ physiological economy) follows the Mendelian law of inheritance, is *not* dependent upon a fundamental difference between these two kinds of flies in *inherent* vitality. This difference, on the contrary, appears merely to be due to the fact that under the environ-

mental conditions represented by the standard fly husbandry of the laboratory (the *A* of our schema) vestigial flies were not able to bring their inherent vitality to so complete expression in duration of life as were the wild type flies under the same conditions.

This result is a specific example of the general principle that the somatic expression of any genetic factor in any particular case is in part a function of the general environmental situation which exists in that case. It has been demonstrated that *under the standard feeding conditions for laboratory bred Drosophila* the gene for vestigial has as a part of its somatic expression a considerably reduced duration of life as compared with the wild type. There are few cleaner-cut examples of Mendelian segregation to be found in the whole literature of genetics than that of *Drosophila* with respect to longevity. Yet the results just described show that the whole of that part of the somatic expression of the vestigial gene which is differential in respect of duration of life disappears under another system of "feeding" wild type and vestigial flies (namely, complete starvation).

An example, from quite a different field, of the general principle that environmental conditions must be optimal for the expression of the character, if reliable genetic conclusions are to be drawn, is afforded by the recent work of Hoffer, who showed that selfed lines of maize made better growth when grown in clay soils, whereas hybrids of the same lines grew better in loam soils.

SEEDLING GROWTH AND LONGEVITY

The manifestations of inherent vitality can be studied in plants even more favorably than in animals. The dry seed of a dicotyledonous plant, like a canteloupe (*Cucumis melo*) let us say, is a complete but undeveloped individual. It contains in the cotyledons, which are morphologically leaves of the preformed plant which the seed includes, stored nutritive material sufficient to carry the seedling on until the nutrition can be obtained by absorption through the roots and by photosynthesis. The cotyledons, and the stored nutriment which they contain, are an integral part, and a very important part, of the total organic pattern of the individual. If now we sterilize such a seed, plant it on a medium which contains no food material upon which the roots can draw, and keep the whole preparation in the dark, the growth of the etiolated seedling which ensues is an expression of the *inherent vitality* (as defined above) of that individual. The seedling must draw whatever nutriment it gets from endogenous sources, which are themselves an integral part of the total organized pattern of the individual. Again we shall be able to discuss the *B* element of our scheme, the organization of the individual, freed from the disturbing influences of *A*.

Now suppose we set up an experiment of the following sort. Long glass tubes, closed at one end like a test tube, are made by the glass blower. In each of these tubes is poured 40 cc. of a 2.5 per cent solution of agar in distilled water. The agar has been purified by repeated washing in distilled water, until all soluble material has been removed from it. The tubes and their contents are then sterilized in an autoclave. After the agar has cooled and set to a jelly there is placed on its surface, with aseptic precautions, one canteloupe seed, which has been specially prepared in the following way. In the first place all the seeds for a given experiment are the produce of a single melon grown the year before in our experimental garden. In this way approximate genetic homogeneity in the ex-

periments is secured. Each seed is individually weighed and measured and the selection of the seeds to be used based upon these quantitative data. Then, under aseptic precautions, the testa is removed from each selected seed. The shelled seeds are then sterilized by immersion for one minute, with stirring, in a 1:1000 bichloride of mercury solution, following by rinsing in sterile, distilled water. The seeds are then soaked for three hours in sterile distilled water, in such a way as to ensure that each seed is not in contact with any other, and that

ing. A richly branched root system develops in the agar substrate. Above it rises a straight unbranched stem, bearing the cotyledons at its top.

The period of growth is followed by the *period of suspended animation*. After growth has ended the seedling remains without visible change for a varying number of days, not growing but still living, with cells in full turgor, and in every way entirely normal in appearance. The plant is living and carrying on metabolism, but it has stopped growing.

The period of suspended animation is

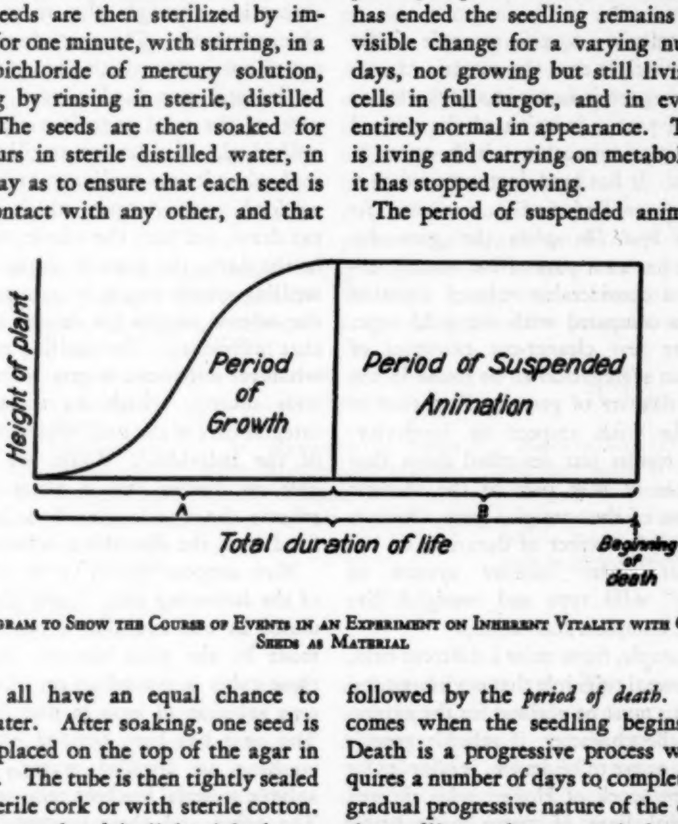

FIG. 8. DIAGRAM TO SHOW THE COURSE OF EVENTS IN AN EXPERIMENT ON INHERENT VITALITY WITH CANTALOUP SEEDS AS MATERIAL

therefore all have an equal chance to absorb water. After soaking, one seed is carefully placed on the top of the agar in each tube. The tube is then tightly sealed with a sterile cork or with sterile cotton. The tubes are placed in light-tight boxes and put in an electric incubator running at 30°C.

What happens in such an experiment is shown schematically in figure 8. In this diagram the horizontal scale represents time and the vertical scale the size of the seedling plant.

There is first the *period of growth*. During this period the seedling is actively grow-

followed by the *period of death*. A time comes when the seedling begins to die. Death is a progressive process which requires a number of days to complete. The gradual progressive nature of the death of the seedling makes a practical trouble in the experiments. It is difficult to decide upon and to read an end-point of total duration of life. The series of events involved in the death of the plant are nowhere sharply and precisely delimited. The stages grade into each other by a gradual continuous process difficult to break up observationally into discontinuous phases, for the simple reason that

death *is* fundamentally and inherently continuous from the time that breakdown starts until the last cell is dead.

We have studied various "end-points," and have found the most reliable and least variable, because capable of being read with the greatest certainty, to be the beginning of death, as evidenced by the first appearance of abnormality of the stem, in the continuous series which in-

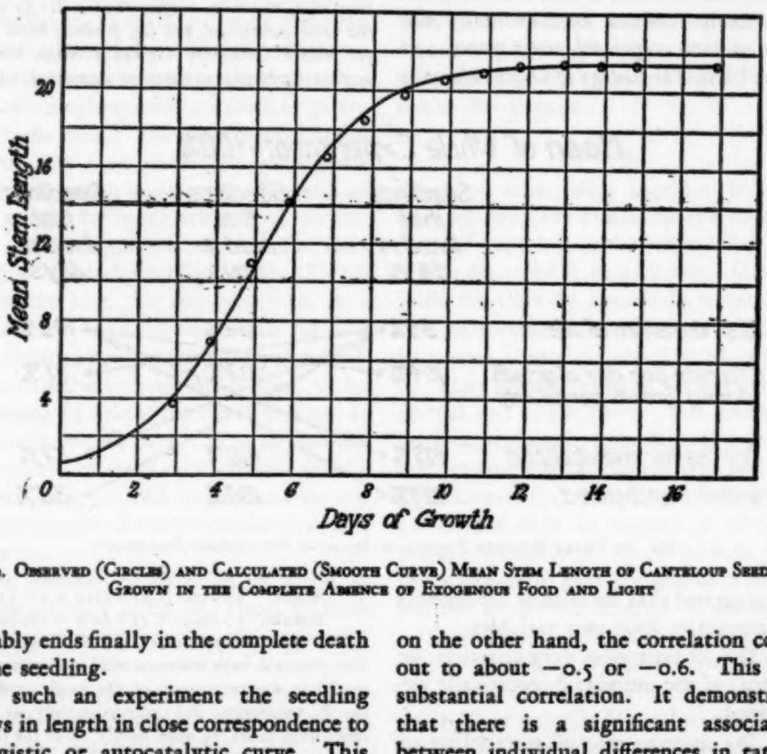

FIG. 9. OBSERVED (CIRCLES) AND CALCULATED (SMOOTH CURVE) MEAN STEM LENGTH OF CANTELOUP SEEDLINGS GROWN IN THE COMPLETE ABSENCE OF EXOGENOUS FOOD AND LIGHT

variably ends finally in the complete death of the seedling.

In such an experiment the seedling grows in length in close correspondence to a logistic or autocatalytic curve. This curve has been found widely useful in describing the course of growth in both individuals and populations. How closely the actual experimental results with the canteloupe seedlings, under conditions of inherent vitality, follow the logistic curve, is shown graphically in figure 9.

The time duration of both the growth period and the period of suspended animation, and therefore by necessary consequence the total duration of life, varies considerably from individual to individual. Now if we determine the correlation between the rate of growth during the growing period (that is, the increase in stem length of the seedling per unit of time), on the one hand; and the total duration of life to the beginning of death, on the other hand, the correlation comes out to about −0.5 or −0.6. This is a substantial correlation. It demonstrates that there is a significant association between individual differences in rate of growth on the one hand and duration of life on the other hand, in this group of seedlings, grown under such conditions that both of these phenomena are necessarily dependent solely upon the inherent vitality of the individual as here defined.

There can be no reasonable doubt as to the correctness of the conclusion that con-

sistent and accordant results will be obtained if inherent vitality, the manifestations of which are dynamic expressions of the biological organization of the individual, be measured by observation either of growth or of duration of life.

The negative sign of the correlation between growth rate during the growth period and total duration of life means that the faster the rate of growth the shorter the duration of life, and *vice versa*. This result confirms experimentally the point of view expressed some years ago in my book *The Biology of Death*, where it was suggested that duration of life depends fundamentally upon two variables:

a. The constitution (organization or pattern) of the individual, genetically determined.

b. The average rate of metabolism or rate of energy expenditure during life.

On this view, if the average rate of metabolism, or of energy expenditure, is high the duration of life will tend to be shortened, while if, for any reason, the average metabolic rate or rate of energy expenditure is low the total duration of life will tend to be prolonged.

Entirely independent experimental confirmation of this result is furnished by the work of MacArthur and Baillie on the mortality of *Daphnia magna*. They find that

> The relative longevity of the sexes may be expressed as varying inversely with their average rates of metabolic activity. The average age at death for males was 37.8 and for females 43.53 days, the duration of life for females exceeding that for males by 14.6 per cent. Now in metabolism, as estimated by heart rate, the males surpass the females by nearly the same percentage, and the product: heart beats per second (weighted average through life) × average age in days at death = a constant, *e.g.*
>
> Males: 4.3 beats × 37.8 days = 161.54
> Females: 3.7 beats × 43.8 days = 162.06
>
> The experimental data thus tend to support the view that a definite endowment of vital energy, potential in the protoplasm of the species and line, may be transformed and expended rapidly, as in the short-lived males, or more slowly, as in the longer-lived females. The evidence so far available indicates also that length of life in *Daphnia magna* has the usual temperature coefficient for a chemical reaction. Other factors being equal, it would seem that, at least in this species, longevity is a function of metabolic rate.

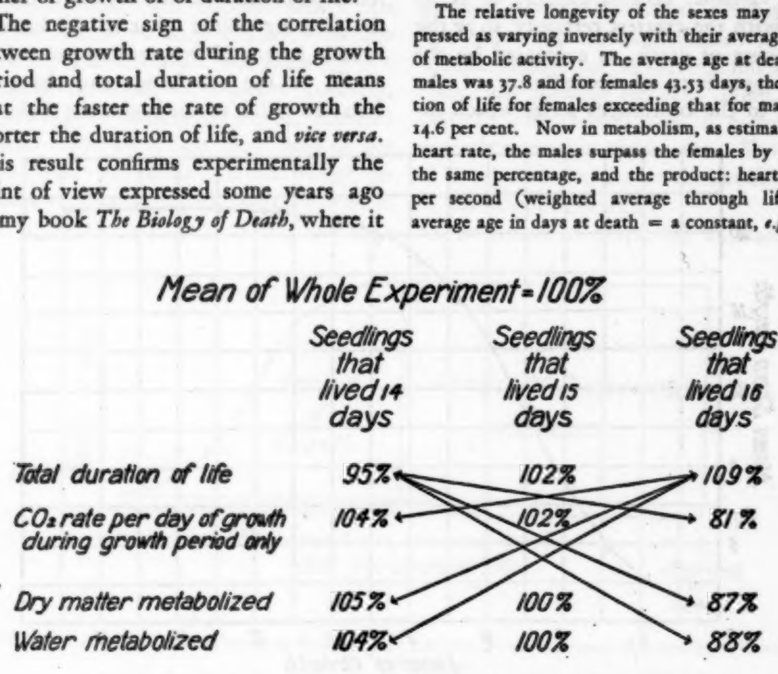

Fig. 10. Chart Showing Results of Seedling Metabolism Experiment

SEEDLING METABOLISM

During the past year we have been carrying on some experiments with cante-

loupe seedlings, which still further confirm and extend our results. To the experimental situation which has been described above, there has been added the determination of the carbon dioxide produced by the respiration of the seedling throughout each period of the experiment, and also determinations of the total metabolic transfer of dry matter from the cotyledons to the stem and roots, and of water from the purified agar substrate to the seedlings. I shall not weary you with a description of the elaborate technique required to measure accurately the respiration of a single cantaloupe seedling growing in the dark. The plant physiologists present know all about the tribulations incident to such endeavors. The rest of you would be bored with their recital. The details must be reserved for publication in a technical journal, but I wish to present here, for the first time, in a preliminary way, some results of one experimental run, which involved 7 seedlings. Of these 7 seedlings 3 lived, to the beginning of death, 14 days; 3 lived 15 days; and one, 16 days. If we express the average condition of each variable for the whole group in this experiment as 100 per cent we then have the results shown in figure 10.

The number of seedlings involved in this experiment is far too small to have anything but suggestive value, taken by themselves. But a great deal more work has been done along the same lines, always with the same results in principle, which will in due time be published in full detail. This particular experimental run is taken for illustration simply for the reason that it was the first definitive experiment in which the hypothesis developed above as to inherent vitality and duration of life was tested biochemically.

The general upshot of all this work is that those seedlings which have a relatively rapid rate of CO_2 production in respiration during the growing period, and which metabolize a relatively large amount of dry matter and of water during growth, live a shorter time in total than do seedlings which have a relatively slow CO_2 rate, and a relatively small metabolic transfer of dry matter and water, during growth. The relatively long-lived plants lived at a slower rate than the relatively short-lived plants. In figure 10 lines are inserted connecting relative duration of life with approximately equal relative metabolic rates. These lines run across the diagram.

SUMMARY

Let us now bring together in summarized form the results of the different lines of experimentation that have been briefly described in this lecture. Starting with the fruit fly *Drosophila melanogaster* and its mutant form called vestigial, we have seen that the normal wild type of fly dies according to a characteristic, normal sort of life curve. But under the same experimental—that is to say, in this case, environmental—conditions the vestigial mutant form has a quite different life curve, not only in respect of absolute average duration of life, which is only about one-third that of the wild type fly, but also in the whole shape of the curve.

Under these conditions of identical environment these differences between wild and vestigial flies behave in inheritance exactly like a simple Mendelian character, when the two kinds of flies are bred together.

At the same time, however, by modifying one element of the environment, the density of population or degree of crowding, it is possible to convert the normal wild type curve over into the vestigial life curve.

This apparent paradox makes it neces-

sary to probe deeper into the matter, which has been done by devising experiments of such a character that we are enabled to study the organization, the constitutional make-up or pattern, of the organism free from the disturbing influence of the necessity normally present in biological work for the organism to derive its energy from sources external to itself. When this is done it at once appears that the apparent genetic difference between wild and vestigial *Drosophila* in respect of duration of life, which so clearly manifests itself in Mendelian experiments, is really only a result of the fact that in a normal environment, optimal for wild type flies in respect of food, vestigial flies are not able to bring to complete somatic expression their inherent potential viability. Vestigial and wild type flies are seen, under these conditions, to have the same inherent vitality. Furthermore, under these conditions, altering the density of population does not alter the shape of the life curve or the average absolute longevity.

With the confusing effects of the interrelationship of heredity and environment thus experimentally cleared away, we are able to plan experiments which will give us some real insight into the basic biological variables which determine longevity. And parenthetically it may be remarked that in a great deal of standard genetic work with what may be loosely called "physiological" in distinction from "morphological" characters, there perhaps inheres the same kind of confusing interrelationship in the effects of heredity and environment which led to the initial paradox in the fly work we have discussed. There is an underlying postulate, usually unrecognized and almost never discussed, implicit in nearly all genetic work. It is that, if in a constant environment A, a difference between two organisms such that one has the character in the condition B and the other in the condition B', segregates in the second filial generation following a cross, the difference between B and B' is to be regarded as genetically determined or caused. But this postulate is only completely valid if it has first been demonstrated that the environmental condition A is equally favorable for the development to complete somatic expression of *both* B and B'.

To come back now to our own trail, it has been possible to show, by experiments with cantaloupe seedlings so devised that we are working solely with inherent vitality, that the duration of life or longevity of the individual varies inversely as the rate of energy expenditure in metabolism during life. In short, the faster an organism lives, the sooner it dies.

This, then, is the conclusion at this stage of a continuing program of experimental research on the biology of life duration or longevity. This conclusion may, and doubtless will, be modified, refined, and extended as the experimental program continues, but I think it is hardly likely to be reversed.

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CRITERIA FOR DISTINGUISHING IDENTICAL AND FRATERNAL TWINS

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THE biological fact that there are two kinds of human twins and twinning phenomena is now universally acknowledged. No one doubts today the distinction between monozygotic or identical twins, who originate from a single fertilized ovum by a process which is apparently a kind of budding or fission in a broad sense, and dizygotic or fraternal twins, who come from two independent ova fertilized and implanted practically at the same time. A criterion for discriminating these two kinds of twins from each other with correctness would be of immense value to geneticists, pathologists and psychologists. There are in fact certain features of twins which, it has been maintained by previous workers in this field, serve this purpose.

THE CHORION AND PLACENTA

The foetal membranes, notably the chorion, and also the placenta in some cases, are often thought to give a very reliable decision as to whether the twins are monozygotic or dizygotic. If each foetus is covered by a separate chorion they are dizygotic, while if they are covered by a common chorion and provided with a common placenta, they are monozygotic. No doubt this rule holds true for a majority of cases. However, certain recent workers like Siemens (1924a, 1925, 1927) and v. Verschuer (1927) claim to have found instances which are at variance with it. Thus, some twins were born with separate chorions, and nevertheless show very close similarity in many physical features, while other twins very different from each other in several characteristics were covered with a common chorion at birth.

Moreover, statistical data, according to these authors, suggest the existence of such exceptional twins. There is a simple method of calculating the approximate number of monozygotic twins among a given twin population, from the number of different-sex twins found in it, which is called Weinberg's differential method. This method is based on the assumption that the sex of one of the dizygotic twins is determined independently of the other; if this is the case, there must be about the same number of dizygotic twins among the same-sex twins as there are different-sex twins, and the rest of the same-sex twins are monozygotic. By this method, the percentage of monozygotic twins has been estimated at from 26 to 36 (according to v. Verschuer's figure); this exceeds more or less the percentage of monochorionic twin-births, which is 14 to 26. It is thus likely that a small percentage of monozygotic twins are born with separate chorions.

Dahlberg (1926) criticizes the above contention of Siemens and states that the abnormal cases mentioned by the latter

author are probably due to some mistake in the diagnosis of the chorion; and moreover, as he maintains, the percentage of monochorionic births among the total twin-births, according to his estimate, conforms very well to the percentage of monozygotic twins among the whole twin population calculated by the differential method.

Whether any small percentage of such puzzling cases as mentioned above exists or not among twin births, accurate information on the foetal membranes is usually lacking for births outside of the hospital.

Thus, we have still to seek for the criterion for classifying twins in their physical and psychical features.

PHYSICAL FEATURES

Of all physical features, our attention is naturally directed first to physiognomy. As Dahlberg remarks (1926), we have a very sharp sense for discriminating slight details of facial appearance, so that the close resemblance of twins in physiognomy to such a degree that even near relatives can not tell them apart, must involve the identity of their various minute facial features to a very great extent. Thus physiognomy can undoubtedly serve as a good criterion for classifying twins. This method, however, has a drawback in that the judgment of the degree of resemblance depends largely on our subjective sense, and is naturally more or less arbitrary. Many workers, accordingly, seek to rely on more objective anthropological measurements and descriptions of other physical characters, such as stature, head form, hair color and form, skin color, blood group, etc.

Muller (1925), among others, has devised a scheme of calculating the a priori chance that given twins are identical on the basis of the data obtained from certain unrelated physical characters of the twins and their siblings like stature, hair form, skin color, etc. Thus, according to him,

> "If there are n sibs altogether (including the twins), a of them falling into class a with respect to a given trait, b into class b, c into class c, etc., the chance that the twins should have been found in the same class is;
>
> $$\frac{a}{n}\frac{a-1}{n-1}+\frac{b}{n}\frac{b-1}{n-1}+\frac{c}{n}\frac{c-1}{n-1}+\text{etc.}$$
>
> If, now, the traits are inherited independently, as they usually will be to a large extent, the chance that two sibs should be in the same class in respect to all of the traits considered is the product of all these chances found in the case of each separate trait" (p. 436).

And the chance that the given twins are identical is approximately $\frac{P}{P+1}$, where $\frac{1}{P}$ stands for the chance that non-identical twins should agree in all the traits. The mathematical ground for the formula has been criticized by Miss Burks (1926) and defended by Muller (1926).

It has been remarked by certain authors that identical twins represent the right and left halves of one individual, and that there is often symmetry reversal in some feature or other. The existence of such symmetry reversal is a sign that the twins are monozygotic. Wilder (1904) and Newman (1917) have expressed their view in favor of this idea. Studies have been carried out by some workers to elucidate this interesting question of the asymmetry and symmetry reversal of twins. Handedness has been studied by Siemens (1924b), Lauterbach (1925), Dahlberg (1926) and v. Verschuer (1927), the direction of head whorl by Lauterbach (1925) and v. Verschuer (1927), the height of testes in scrotal sac by v. Verschuer (1927), besides other characters such as the mode of clasping hands and functional superiority of one leg examined by Dahlberg

(1926), asymmetry in eyes, ear-form, etc. by v. Verschuer (1927), and the occurrence of naevi by Siemens (1924b).

The result is somewhat different according to the characters considered. But symmetry reversal is rather frequent among identical twins for nearly all these characters. This is especially the case with handedness (Lauterbach, 1925; Dahlberg, 1926; v. Verschuer, 1927). But the puzzling fact is that left-handedness is decidedly more frequent among fraternal twins as well as among identical twins, than in the general population. Left-handedness ought, therefore, to be considered a phenomenon directly connected somehow with twinning in a general sense, and not necessarily with the special kind of twinning bringing about identical twins.

Siemens' diagnosis of twins (1924b, 1927), which has since been used rather extensively, is based on a good many physical features, that is

"A. Traits which agree in one-egg twins almost always and almost completely; in two-egg twins only rarely: 1. hair color and form, 2. eye color, 3. skin color, 4. downy hair of the body; B. traits which agree in one-egg twins, and which usually vary more widely among two-egg twins: 5. freckles (location of), 6. appearance of blood in the skin (teleangiectasis, cutis marmorata, acroasphyxia), 7. follicular processes (lichen pilaris, acne), 8. tongue (furrowed or not) and teeth; C. traits in which one-egg twins usually, two-egg twins only rarely show strong resemblances to each other: 9. form of face (physiognomy), 10. form of ear, 11. form of hands (and of nails), 12. body build;" besides "13. mental make-up (school standing, character, talent), 14. illness and abnormalities, 15. traits which are the bases of special methods of investigation (finger prints, microscopic comparison of the capillaries, refraction of the eyes, blood groups and so on" (Siemens, 1927, pp. 205–207).

There is no doubt that this scheme is more comprehensive and naturally safer than others hitherto proposed. It has, however, a rather limited application to twins among races in which the hair-color and form, eye color and skin color are subject to only a slight variation as, for instance, the Mongolian race.

Dahlberg (1927), lastly, puts emphasis on the usefulness of the ear form for this purpose.

FINGER, PALM AND SOLE PRINTS

Galton (1892) was the first to recognize the close similarity existing between the friction-ridge patterns of fingers of some same-sex twins. He compared the prints of fore, middle, and ring fingers of the right hand of 34 pairs of twins, and found that in some of the pairs the agreement of the patterns was so close that they should be assigned to the same class according to his classifying scheme, while in others the correspondence was only partial and in still others no correspondence was found.

Wilder (1904, 1908, 1919) worked on some 50 sets of palm and sole prints of twins, besides 16 sets of finger prints, and came to the conclusion that

"the friction-skin configuration of twins corroborates the conclusions based upon the general physical appearance, that there are two distinct types of human twins, duplicate (or identical) and fraternal." "The correspondence in the friction-skin configuration is confined to the general plan of the surface as a whole and does not extend in the least to finer details, the 'minutiae' of Galton." "In duplicate twins there is, in both hands and feet, a marked correspondence between the two sides, so that the right and left hands of each twin correspond as completely as do the right or the left hands of the two individuals. All four of the hands involved are thus duplicates of virtually the same picture, and the same phenomenon is shown in the four feet" (1919, p. 2).

Poll (1914) studied finger prints of 83 pairs of presumably identical twins besides two sets of triplets and one pair of pygopagus. In no case did he meet with a correspondence of all fingers even as regards the type of pattern. Rarely nine fingers were similar and one different.

Ganther and Rominger (1923) worked

on the finger and palm prints of five pairs of monozygotic and forty-two pairs of dizygotic twins whose placentas had been examined at birth. They found that the corresponding fingers of identical twins are usually very similar, to such an extent that at least seven, and at most nine, fingers have the same type of patterns, but at least one finger shows dissimilarity. The palm patterns of hands of identical twins show even closer resemblance; the similarity of the same side especially is very great. The palms of the dizygotic twins, on the contrary, are never so much alike. Accordingly he expressed his view that the palm prints give the most reliable criterion, next to the placenta, for identifying monozygotic twins.

Bonnevie (1923, 1924), in her studies on finger prints, examined the degree of similarity found between same-sex twins with 16 pairs of presumably fraternal and 15 pairs of presumably identical twins as material. She estimated the degree of similarity between each pair according to her own scheme, and found that the correlation of pattern-values between fraternal twins is very similar to that between ordinary brothers and sisters, whereas the correlation between the identical (?) twins is much higher, in fact so much as to "fully equal and even slightly exceed that found for the values of right and left hands of identical twins, or of single persons" (1924, p. 100).

Leven (1924) studied the finger prints of 23 pairs of same-sex twins including 15 pairs of presumably monozygotic and 8 pairs of presumably dizygotic twins. Much more difference, in the type of patterns, as well as in the number of ridges and in other details, was found among the latter than among the former kind of twins.

Lauterbach (1925), in his study on 212 pairs of twins, consisting of 149 pairs of same-sex, and 63 pairs of different-sex twins, examined the palm patterns. Special attention was given to the palm patterns of the twins showing symmetry reversal in handedness and in the whorl of the head hair. His conclusion was that "palm patterns afford no certain means of identifying monozygotic twins. Unlike-sex pairs of twins may show identity of palm patterns and reveal symmetry reversal" (p. 567).

Montgomery (1926) worked on the sole patterns of 57 pairs of same-sex, and 30 pairs of different-sex twins. He concluded that "the presence of identical patterns on the soles of a pair of twins might point to their monozygotic origin, but, as Newman states, their absence does not disprove it" (p. 299).

Kuragami (1926) examined finger-prints of 15 pairs of same-sex twins and 5 pairs of different-sex twins, and found, among other things, that in two pairs of the same-sex twins the ridgecount of the prints gave precisely the same value.

Obonai (1926) carried on a psychological and anthropological study on some 200 pairs of twins. He also examined the finger prints of these twins, and called attention to the fact that some pairs of same-sex twins which would be taken as identical judging by their resemblance in physiognomy and in physical and psychical characteristics, may have very unlike finger patterns.

Kishi (1927) collected finger prints of 60 sets of twins including 49 pairs of same-sex and 11 pairs of different-sex twins, and has found, among other things, that the finger prints of different-sex twins are more variable than those of same-sex twins.

Apart from works dealing with only a few pairs of twins, the above is, I believe, a nearly comprehensive review of the literature relating to the finger, palm, or

sole patterns of twins which has appeared to this day.

MY STUDY

The material which has formed the basis of my study consists of 9 sets of palm, sole and finger prints and 55 sets of palm and finger prints of same-sex twins, 9 sets of palm and finger prints of different-sex twins and one set of palm and finger prints of male triplets, obtained mainly from among the school children of the city of Kyoto. This material has been greatly supplemented by the collection of Mr. Obonai, who generously put them all under my examination. These include finger prints of 166 pairs of same-sex twins and 30 pairs of different-sex twins obtained from among the school children in the city and suburbs of Tokyo; and some are accompanied by palm prints.

The formulation of the patterns and ridges has been done largely after Wilder's scheme with a slight modification (Wilder, 1904, 1916; Wilder and Wentworth, 1918). Especially, it has been found advisable to take into consideration as many available characteristics of the patterns as possible. Thus, for finger patterns, besides the number of ridges, certain other characteristics, for instance, the ratio of the height and breadth and the tendency towards twisting mentioned by Bonnevie (1923, 1924), and also the length of each ridge, have been considered. For palm patterns, the number of ridges intervening between the main lines has been counted and the various shapes of the hypothenar pattern recorded. In addition to the data obtained from the examination of the above material, I have consulted, for drawing general conclusions, the data in the works by previous authors, especially by Wilder (1904, 1919), Poll (1914), Ganther and Rominger (1923), Lauterbach (1925), Montgomery (1926), Kuragami (1926) and Kishi (1927).

FIG. 1. BROTHERS INCLUDING A PAIR OF IDENTICAL TWINS
The twins were born with a common chorion and placenta. Both are graduates of the Kyoto Imperial University.

Lack of space prevents me from going into the details of the study, and I can only

give very briefly a general summary of the main results.

My study has revealed that the finger, palm and sole prints of the twins whose monozygosity is evident on various grounds, such as the similarity of physiognomy, body build and school standing, resemble each

Fig. 2. Monozygotic (?) Girl-twins, from Mr. Obonai's Collection of Photographs of Twins

other closely, much more than the prints of the different-sex twins or of the same-sex twins who are identified as dizygotic. To give a rough idea of the contrast of the two kinds of twins, the finger prints of the monozygotic twins very seldom show differences in the type of pattern (whorl, twin loop, double loop, ulnar loop, etc.) in more than two pairs of corresponding fingers, whereas in dizygotic twins the difference is met with usually in more than two pairs of corresponding fingers.

The similarity of the pairs of monozygotic twins is especially marked between the fingers, palms or soles of the same side (right or left), so that very often the hands or feet of the same side of different individuals resemble each other more closely than the two hands or feet of the same individual. To represent in symbols, let r and l stand respectively for the right and left hand or foot of the one twin A,

Fig. 3. Boy-girl Twins very Different in Body Build; Children of a Primary School of Kyoto

and r' and l' respectively for A', the identical twin of A, then

$$r - r' \text{ (or } l - l') < r - l \text{ (or } r' - l')$$

Such a condition, so far as I have ascertained, is met with in no case of different-sex twins nor of same-sex twins whose dizygosity is undisputed. So that this may serve as a criterion for identifying many monozygotic twins.

To my mind, the difference in pattern of the two hands or feet of the same indi-

Fig. 4a

Fig. 4b

Fig. 4. Monozygotic (?) Triplets

They are now 24 years old; enjoy good health and stood high in class; all served in the army

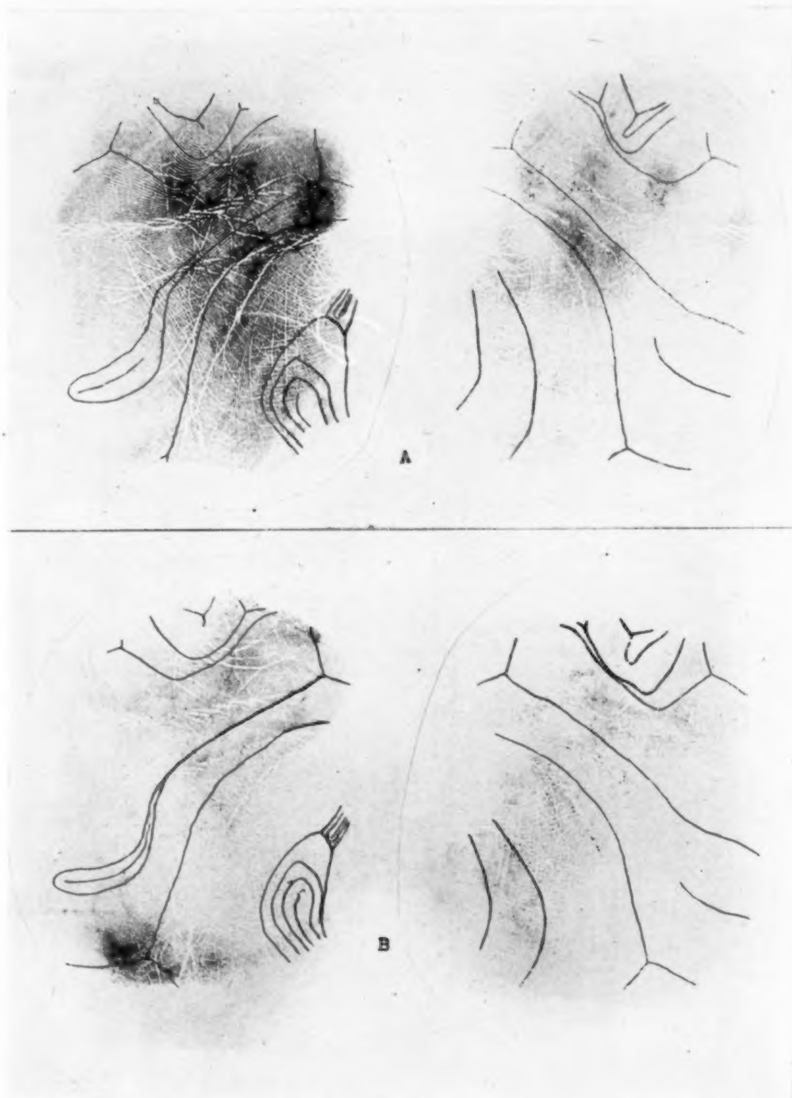

FIG. 5. PALM PRINTS OF A PAIR OF MONOZYGOTIC (?) TWINS
Note the close similarity of the patterns of hands of the same side

FIG. 6. SOLE PRINTS OF ANOTHER PAIR OF MONOZYGOTIC (?) TWINS
Note the close similarity of the patterns of soles of the same side

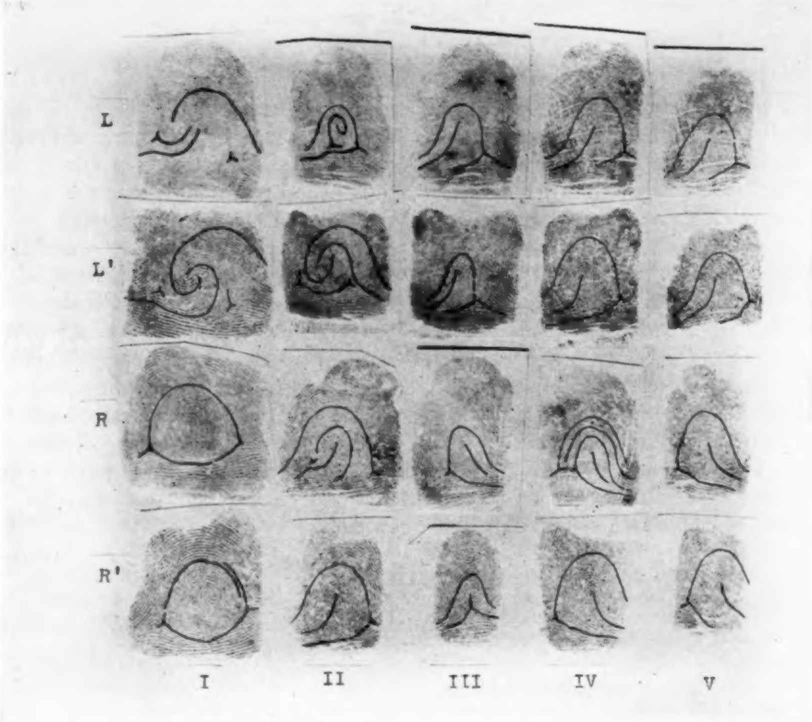

Fig. 7. Finger Prints of the Twins in Figure 1

The patterns are rather variable for monozygotic twins. Note the similarity of the patterns of thumbs of the same side.

Fig. 8. Monozygotic (?) Girl-twins

Both are very popular athletes of high standing. One of them (left) once created a world record in 100 meter race.

vidual is, at least in part, due to the specialization of the right and left halves of the body, in the same sense as right or left handedness or the functional superiority of one leg, rather than to the patterns transcending the limit of control of the hereditary factor. The hands or feet of the same side of monozygotic twins, on the contrary, are virtually the duplicates of each other; and it is but natural that they resemble each other more closely than the hands or feet of one individual.

It can not be disputed, however, that certain same-sex twins who are known to have been born with a common placenta and who resemble each other very closely in physiognomy and body build, have dissimilar patterns on more than two pairs of fingers or on palms or soles. Also it is by no means rare that the general rule for patterns of monozygotic twins stated above does not hold good. The dissimilarity of the patterns or the nonconformity of them to the rule, therefore, does not necessarily disprove the monozygosity of the given twins. Thus the method of distinguishing the two kinds of twins by means of such patterns has its limitations. But, if used in collaboration with other methods, it will prove to be a very useful and reliable one for classifying twins.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* The Quarterly Review of Biology, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

MORGAN ON ENTWICKLUNGS-MECHANIK

Being a review of *Experimental Embryology* by Thomas Hunt Morgan. New York (Columbia University Press) 1927. $5\frac{7}{8}$ x $9\frac{1}{8}$; xi + 766. $7.50.

By S. R. Detwiler, Columbia University, and H. B. Adelmann, Cornell University

Embryology as a scientific discipline is comparatively young. As a matter of fact, it is just a century old, since it may be said to have begun its modern epoch in 1828 with the publication of von Baer's monumental work, *Über Entwickelungsgeschichte der Thiere. Beobachtung und Reflexion.* The modern reader of this classic can only marvel at its high level of accuracy and the prophetic insight of its author.

For more than fifty years embryology remained, almost of necessity, a purely descriptive science, but with the publication of Wilhelm Roux's research concerning the time of determination of the principal axes of the frog embryo, *Ueber die Zeit der Bestimmung der Hauptrichtungen des Froschembryo*, in 1883, and his vigorous advocacy of the experimental approach to the solution of the problems of development, embryology may be said to have entered upon a new era.

This new "Zweig der Wissenschaft" was termed by Roux developmental mechanics (*Entwickelungsmechanik*). Driesch prefers to call it developmental physiology (*Entwickelungsphysiologie*), thus avoiding a mechanistic implication, but in English Experimental Embryology is the designation usually preferred. In the beginning Entwickelungsmechanik met with many obstacles, and its fond parent was frequently called upon to justify its existence and to shield it from attacks of the scornful. This he lost no opportunity to do. Numerous programs of the work were issued (1885, 1889, 1892, 1897, 1905, etc.) outlining the field. He predicted a brilliant future for the child and it is only just to say that his confidence has been abundantly justified.

As conceived by Roux, the goal of Entwickelungsmechanik is a complete causal analysis of every developmental process. While recognizing that some causal relationships might be deduced from observation, Roux laid special stress upon the value of experiments, of which he recognized four principal types: (1) the blind experiment (i.e., the I-wonder-whether-something-interesting-might-

happen-if-I-should-do-thus-and-so type of experiment); (2) the descriptive (*formal-analytische*) experiment in which no reaction is called forth in the object, (3) the indefinite causal experiment and (4) the causal-analytical experiment;—the latter being the highest type. In 1889 Roux was led to remark that "The causes of organic formations (*Gestaltungen*) are at present more unknown to us than the causes of the movements of the heavenly bodies were to mankind before Newton."

Experimental embryology is thus, as sciences go, very youthful—only forty-five years of age—a veritable youngster, and like all youngsters it is apt to be intolerant. It is prone to assume a disdainful attitude toward mere morphology, and frequently implies that its achievements are of a higher order than those of descriptive embryology. However, its more thoughtful devotees realize that, after all, there is but one science of embryology; that description must precede intelligent experiment and, furthermore, that there are many aspects of development that are not yet susceptible of experimental treatment. The importance and the need of experimental analysis must, however, be apparent to everyone.

In the forty-five years since Roux's experiment on the axes of the frog embryo, a truly enormous mass of literature dealing with experimental embryology has accumulated. Each year sees an increase in the production of literature over the preceding year, so numerous have workers in the field become. As a result, it is difficult for the beginner and even for the seasoned worker to keep fully informed of the current advances, and it becomes more and more difficult for the novice to orient himself in the subject. Summaries of research programs and reviews of the whole field from time to time are therefore exceedingly valuable.

In 1897 Professor Morgan published *The Development of the Frog's Egg. An Introduction to Experimental Embryology*. It was an admirable work, the first of its kind in the English language. At that time Roux's Archiv für Entwickelungsmechanik had been in existence only two years and but five volumes had appeared, and the Journal of Experimental Zoölogy—to mention but two sources of publication—had not yet been founded. It was then possible to give a very adequate treatment of the subject, with particular reference to the frog, in a volume of 192 pages, including a 13 page bibliography.

Since the appearance of Professor Morgan's first summary, there have, of course, been many important advances. Since 1897 more than sixty volumes of Roux's Archiv and fifty of the Journal of Experimental Zoölogy have been issued. Important research programs have been initiated and prosecuted, in many instances with gratifying success. To mention only the most fruitful, one might cite: (1) the important researches of Professor Harrison on the growth of the nerve fiber, his discovery of tissue culture and the important series of analyses of the development of the limb and other organs carried out by himself and his students, (2) the remarkable researches of Spemann and his students on the "*Organizator*" and the determination of the various organs and tissues of the Amphibian embryo, (3) the studies of artificial parthenogenesis by Loeb, Morgan, Bataillon, Brachet and others, (4) studies on cell lineage by Wilson, Conklin and others, (5) Child's development of the theory of physiological gradients, (6) the researches on cytoplasmic localizations by Conklin, Brachet and others, and (7) the development of the method of vital staining as employed by Goodale, B. G. Smith, Vogt and Goerttler in the study of the movements

of cells during gastrulation in the Amphibian, and by Detwiler and others in studying the fate of transplanted tissues. The list is not complete, nor does it necessarily cite in order of merit.

Besides several digests in foreign languages, a number of summaries in English are available. There may be mentioned Jenkinson's *Experimental Embryology* (1909), de Beer's succint and useful *Introduction to Experimental Embryology* (1926) and, particularly, the masterly chapters devoted to this subject in Professor Wilson's *The Cell in Development and Inheritance* (1925).

Since the publication of his work on the development of the frog, Professor Morgan has made a long and profitable excursion into the field of genetics and has become so intimately identified with this field that many younger investigators are apt to forget that he has been a prolific contributor to experimental embryology *sensu strictu*. In fact, he probably considers, and justly too, that he has been working in experimental embryology all the time.

And now Professor Morgan, after some years spent in pursuit of the gene, presents us with another stimulating review of experimental embryology, which has added importance in that it combines the viewpoints of the embryologist and geneticist. This time it is a volume of 766 pages containing a bibliography of 100 pages. It covers only the earlier phases of development. He promises a future volume which will consider the "more obviously physiological changes" of development, growth, reflex actions, tropisms, sex determination, embryonic grafting, influence of environment on the embryo, the source of the energy of development, etc.

As a whole, the present volume may be characterized as an eminently readable summary and analysis of the outstanding developments in the field surveyed. There are twenty-five chapters. The first is an interesting discussion of the experimental method. This is followed by seven chapters dealing with the problems connected with fertilization. There are others devoted to the physico-chemical changes in the egg after fertilization, the mechanism of cleavage, the establishment of symmetry and the origin of asymmetry, localization before cleavage and the redistribution of the visible materials of the egg by centrifuging, the development of whole or partial embryos from isolated blastomeres, the mechanics of organ formation, the fate of cells and their location, the fusion of two eggs to produce one embryo. There is a long chapter on artificial parthenogenesis and three chapters are devoted to the chromosomes of the egg and their division, the Mendelian inheritance of embryonic and larval characters and the development of species hybrids.

It is only natural that the chromosome and the gene figure prominently in the book. Professor Morgan has always realized that an adequate theory of heredity must at the same time offer a satisfactory explanation of the differentiation of the embryo. In discussing this question in *The Mechanism of Mendelian Heredity* in 1923 he stated (p. 280) that

> The cause of the differentiation of the cells of the embryo is not explained on the factorial hypothesis of heredity. On the factorial hypothesis the factors are conceived as chemical materials in the egg, which, like all chemical bodies, have definite composition. The characters of the organism are far removed, in all likelihood, from these materials. Between the two lies the whole world of embryonic development in which many and varied reactions take place before the end result, the character, emerges. Obviously, however, if every cell in the body of one individual has one complex and every cell in the body of another individual has another complex that differs from the former by one difference, we can treat the two sys-

tems as two complexes quite irrespective of what development does so long as development is orderly.

It is sometimes said that our theories of heredity must remain superficial until we know something of the reactions that transform the egg into the adult. There can be no question of the paramount importance of finding out what takes place during development. The efforts of all students of experimental embryology have been directed for several years toward this goal. It may even be true that this information, when gained, may help us to a better understanding of the factorial theory, we cannot tell; . . . . Although Mendel's law does not explain the phenomena of development, and does not pretend to explain them, it stands as a scientific explanation of heredity, because it fulfills all the requirements of any causal explanation.

He makes substantially the same statement in his *Theory of the Gene* (1926, p. 26). But in spite of the fact that he disclaims any pretension to explain differentiation on the basis of the gene theory, Professor Morgan usually gives some indication of his feelings on the subject. For instance, in 1923, he made this statement (p. 43): "Mendelian factors are not sorted out . . . . differentiation is due to the cumulative effect of regional differences in the egg and embryo, reacting with a complex factorial background that is the same in every cell."

It was with particular interest, therefore, that we examined this latest book of his to ascertain whether his ideas on this matter had been clarified and whether in this book dealing primarily with experimental embryology he would attempt to bring the theory of the gene into some closer harmony with the observed course of embryonic differentiation. It will perhaps be helpful to summarize in the briefest fashion what Professor Morgan has termed the theory of the gene, with special reference to the problem of differentiation and disregarding such aspects as linkage, etc. The theory states that the characters of the individual are represented in the chromosomes of the egg by minute entities termed the genes, which are arranged in linear order. Each gene may affect the development of many characters and the interaction of all the genes may be involved in the manifestation of any particular character. The genes are present in pairs, the members of each pair separating during maturation of the germ cell, but during the ordinary mitoses each gene is divided equally so that the daughter cells are factorially identical. It may be added that cytological evidence seems to indicate positively that the somatic mitoses are quantitative so far as the nucleus is concerned and most observers accept this as an establish fact. The problem, then, is how, with identical factorial equipment, differentiation is started, and how, when once initiated, it is brought to completion.

There would seem to be at least three factors to be considered, (1) the nucleus, (2) the cytoplasm, (3) the environment. Investigators have attempted to answer the question in different ways. The importance of the cytoplasmic localizations of the egg have been stressed, the external environment of the developing egg has been emphasized as important, and for others the nucleus is the most important element. For instance, Child has expressed himself as follows: " . . . . development of the individual represents the reaction of the factorial complex to environmental factors. This seems to be Conklin's viewpoint ('22) and it is essentially the viewpoint of the present book, according to which the physiological gradient constitutes the primary regional differential, to which the factorial complex reacts." Conklin (*In* Cowdry, *General Cytology*, '24, p. 600) emphasizes the importance of the cytoplasm as follows:

Given a definite polarity, symmetry, and pattern of the egg, all other differentiations of ontogeny could be explained as due to the interaction of non-

differentiating genes on different parts of the cytoplasm; but there is no mechanism by which embryonic differentiations could come from the action of non-differentiating genes on a homogeneous cytoplasm. The genes or Mendelian factors are undoubtedly located in the chromosomes, and they are sometimes regarded as the only differential factors of development, but if this were true these genes would of necessity have to undergo differential division and distribution to the cleavage cells, as Weismann maintained. Since this is not true it must be that some of the differential factors lie outside of the nucleus, and if they are inherited, as most of these early differentiations are, they must lie in the cytoplasm.

Rabl ('06) conceived of differentiation as brought about by a continuous interaction between nucleus and cytoplasm,—the primary germinal localizations (organ forming stuffs) of the cytoplasm furnishing the starting point. According to him both nucleus and cytoplasm are progressively changed during the process of differentiation.

Wilson, on the other hand, throws the entire responsibility upon the nucleus. "Heredity," he says, "is effected by the transmission of a nuclear preformation, which in the course of development finds expression in a process of cytoplasmic epigenesis."

Loeb ('16) viewed the cytoplasm of the egg as " 'the embryo in the rough,' carrying the genus—or even the species—heredity, while Mendelian heredity adds only the finer details to the rough block." Jenkinson ('17) adopted a similar view, holding that the larger characters are transmitted by the cytoplasm, the smaller by the nucleus. Conklin is more specific. "We are vertebrates because our mothers were vertebrates and produced eggs of the vertebrate pattern; but the color of our skin and hair and eyes, our sex, stature and mental peculiarities were determined by the sperm as well as by the egg from which we came." But as Wilson further says, "These statements are rhetorically effective, but will not stand the test of critical analysis . . . . the cytoplasmic organization of the egg *is itself the product of an antecedent process of epigenetic development* in the course of which, as we have every reason to believe, the chromosomes have played their part,—thus the chromosomes are as much concerned in the determination of the so-called 'preformed' or cytoplasmic characters as in any others."

Professor Morgan's position is very similar to that of Wilson. Starting with the assumption of a chromosomal architecture as outlined above, he brings out the following points: (1) There is no relation between the arrangement of the genes and the arrangement of the parts differentiated from the egg. (2) The genes remain intact throughout development. There is no evidence for assuming that they are altered by successive cytoplasmic differentiations. (3) There is no basis for assuming that the genes become active in a particular order nor can it be stated whether all the genes are active continually or whether some are more active than others at certain periods.

In short, about all that Professor Morgan feels sure of is that "the genes may change the cytoplasm and the cytoplasm then acts in a specific way" (p. 8).

How the chromosomes, or rather the genes that are their essential constituents alter the cytoplasm of the cells is unknown. There is at least no evidence opposed to the view that they do this by chemical processes. It is impossible to suppose that the genes themselves could be thrown off and could pass through the nuclear membrane into the cell. . . . . It is not so difficult to imagine that through their activities chemical substances are produced that find their way into the cytoplasm either at the time when the nuclear wall is dissolved and nuclear sap set free, or possibly by diffusion through the nuclear walls. (p. 198).

The genes may be influential in the formation of catalytic materials but are probably not themselves enzymes.

The evidence from matroclinous in-

heritance seems to indicate that the "genes affect the cytoplasm, not immediately in a dynamic sense, but rather by some material product that is set free from the genes into the cytoplasm" (p. 655). That there is a time element involved in the action of the genes is also indicated by other hybridization experiments, notably those of Driesch on the sea urchin.

Professor Morgan takes a decided stand against assigning organ forming properties to the various regions of the cytoplasm. While he believes that at the beginning of development the cytoplasm probably contains certain factors which initiate development, possibly determining the cleavage type, he concludes from the evidence furnished by the cleavage of egg fragments that the segmentation pattern is not foreshadowed or predelineated in the protoplasm but that the form of cleavage appears *pari passu* with the development of the mitotic spindle.

He is justly emphatic in his assertion that the visible inclusions of the cytoplasm have no organ-forming function since they may, in many types of eggs, be displaced without altering the course of development. "It does not follow, of course, that there may not be other substances that do have a determinative influence on development" (p. 493). In commenting upon the results of Conklin's experiments in which the eggs of *Styela* were placed in capillary tubes and centrifuged with the consequent formation of abnormal embryos with dislocated larval parts, he is inclined to believe that alteration of the cleavage by compression may be responsible. "Whether the yellow pigment can be separated by centrifuging from the cytoplasm in which it lies, and may then determine the local differentiation of a region, must first be demonstrated in order that crucial evidence of their differentiating function may be established" (p. 534).

In discussing spiral cleavage, a type in which the successive cleavages are more or less rigidly predetermined so that "predictable regions of the egg pass into definite cells," he states that "The alternate changes from right to left and then from left to right, etc., that are characteristic of these divisions can hardly be due to the presence of corresponding regional substances already laid down in the egg. . . . . The mosaic character of the cleavage with its accompanying localization of differentiating factors is something given, but not preformed, in the unsegmented egg" (p. 417). In other words, the various cytoplasmic regions of the egg are conceived of as predetermined in many cases, but not prelocalized.

Just what is implied by the term "differentiating factors" is not entirely clear. In certain cases, as he points out, the character of the cytoplasm seems to determine the character of the differentiation of the regions of the body as, for instance, in certain insect eggs, and as is indicated by Boveri's experiment of centrifuging the eggs of *Ascaris*, certain of Spemann's constriction experiments on *Triton*, etc.

He points out, however, that "even in such eggs where the cytoplasm plays an important rôle in determining the regional differentiation of the embryo, the character of the nuclei is also determinative for those characters that depend on their constitution" (p. 424).

It is interesting to note that symmetry and asymmetry are discussed without reference to Child's theory of physiological gradients. Professor Morgan believes that symmetry, in many cases, is impressed upon the egg by outside influences and would be loathe, we judge, to assume that it is due to an inherent property of the protoplasm in any case. We find ourselves in hearty sympathy with his statement

that while such phrases as polarity, symmetry, organ-forming germ regions, morphogenetic processes and differential cleavages may be useful when used in a descriptive sense, they become deceptive when employed as if something were explained by them. We are, after all, far from understanding the essential nature of symmetry. At present we may only describe it as it is normally manifested with its experimental alterations. Its cause we may never understand. It is, as Bateson suggested, essentially organismic pattern and may very likely have its basis in protoplasmic or molecular pattern.

For Professor Morgan, then, development would consist largely in the nuclear domination of the cytoplasm, which is responsive on the one hand to the nucleus and on the other to its external and internal environment.

One of the most interesting sections of the book is that dealing with the mutual interactions of the embryonic organs upon one another. Herbst deserves the credit for having first in 1901 clearly emphasized the importance of this field. In his *Formative Reize in der thierischen Ontogenese* he listed and discussed a number of examples of external and internal formative stimuli in ontogeny. This aspect of development was for many years more or less neglected and it is only within recent years that the work of Spemann and his students has again focused attention upon it. The fact that a neural tube or even an eye can be induced to form from belly ectoderm by an underlying implant of the roof of the archenteron or a piece of neural plate, or that a more or less perfectly organized embryo can be induced to form by implanting the dorsal lip of the blastopore, has revealed again in a most striking manner the mutual influence of embryonic parts and makes us suspect that there are undoubtedly others just as important of which we are unaware. Whether Spemann's conception of an "*Organizator*" controlling the differentiation of the embryo will stand is, perhaps, doubtful. The experiment, as Professor Morgan points out, may, at any rate, be interpreted as proving that "the formation of the neural plate depends on the presence beneath it of chorda-mesoderm and that the ectoderm of the upper hemisphere is totipotent in its responsiveness to this material."

As regards the subject of artificial parthenogenesis, a very complete summary of the work is given. The interpretation of results in this as in many other fields is still unsatisfactory. "The fact that unfertilized eggs may be induced to develop into normal embryos by artificial agents of the most diverse kind, rather than the hypotheses to account for the change, is the outstanding feature of all this work" (p. 581).

Professor Morgan is hopeful that ultimately we shall find a physical, chemical or physico-chemical explanation of all developmental phenomena. It is entirely possible that one day we shall understand fully the chemical and physical aspects of fertilization, cleavage, gastrulation and differentiation, but there would still remain to be explained the configuration of physical and chemical processes that is characteristic of the development of each organism. As Professor Kingsbury has put it

> Life in an organism today is like a tapestry in which the threads of warp and woof are woven into a pattern of exceeding intricacy and delicacy whose weaving has been going on since the beginnings of life. You may analyze the threads of process as they run in and out today in terms of chemistry and physics but the pattern stands as a history of the past and the weaving is still largely a secret of the ages.

The pattern of the genes may be cited as an example. We may describe the con-

stellation of genes peculiar to the germ-plasm of each species but it will be long before we have a causal explanation of the gene pattern of each particular germ-plasm.

In surveying the status of experimental embryology today one cannot fail to be impressed with the fact that as yet but few causal explanations of developmental processes have been established. Only a small percentage of the experiments described are really causal-analytical in Roux's sense; the bulk of them would have to be described as descriptive experiments and not a few would fall into his category of blind experiment. However, the main service of many experiments, as Professor Morgan has pointed out, has been to reveal new possibilities and the outlook for further advance has never been brighter then at present. One of the great services which Professor Morgan has rendered us in writing his book has been to point out clearly the limitations of many experimental procedures and to suggest other attacks and new problems for solution. The book will prove therefore, a stimulus to many future types of work. We look forward eagerly to the second volume.

Fortunately, perhaps, von Baer's statement is as applicable today as it was in 1828:

> Noch manchem wird ein Preis zu Theil werden. Die Palme aber wird der Glückliche erringen, dem es vorbehalten ist, die bildenden Kräfte des thierischen Körpers auf die allgemeine Kräfte oder Lebensrichtungen des Weltganzen zurückzuführen. Der Baum aus welchem seine Wiege gezimmert werden soll, hat noch nicht gekeimt.

BRIEF NOTICES

EVOLUTION

THE EVOLUTION OF MAN SCIENTIFICALLY DISPROVED. *In 50 Arguments.*
By William A. Williams.
Rev. William A. Williams
1202 Atlantic Ave., Camden, N. J.
$1.00 5 x 7½; 127

The Reverend Dr. Williams has written such a book as to justify his inclusion in our Fundamentalist Portrait Gallery. We take great pleasure in presenting him to the readers of The Quarterly Review of Biology. He is an Ex-president of Franklin College, Ohio, author of "Early American Families," "Silver Tones," "Song Jewels," etc.

The Evolution of Man Scientifically Disproved was first published in 1925, and republished, in a revised and "corrected"

William A. Williams, D.D.

edition of 20,000 copies, in 1928. So it can be seen that the book has had at least a moderate success. And this success seems to us warranted. For the book is by a long way the most amusing Fundamentalist tract that has come our way. What makes it amusing is that its technique is so pesky mean. The strategy is to discuss the numerical consequences of various general statements which have been made by scientific men regarding some of the variables involved in the arguments in favor of evolution. In all controversial technique one of the most devilish, and often devastating, tricks is to set forth solemnly the simple numerical results which necessarily (or supposedly necessarily) follow upon general statements. When someone engrossed in a particular line of evidence which he has been studying says casually that man has been upon the earth one million years, or one hundred thousand years, or some other long time, he usually overlooks the fact that a zealous and ingenious person can figure with pencil and paper about this statement in a whole lot of ways that its originator never thought about at all. Sometimes the consequences of such purposeful arithmetic may be embarrassing in high degree. It was by this technique that the good Bishop Colenso opened the flood gates of Modernism and the Higher Criticism when he turned his diabolical arithmetic loose upon the Pentateuch.

It is again precisely this sort of thing that the Rev. Dr. Williams has done to the evolutionists. His book is divided into three parts. The first part has for its general title "The Evolution of the Human Body Mathematically Disproved;" the second part, which, along with the third, appears to have been written at some later date than the first, has for its title "Evidence Answered;" finally, the third part has to do with "The Soul."

The initial calculation runs this way:

> The population of the world, based upon the Berlin census reports of 1922, was found to be 1,804,187,000. The human race must double itself 30.75 times to make this number. This result may be approximately ascertained by the following computation:
>
> At the beginning of the first period of doubling there would just be two human beings; the second, 4; the third, 8; the fourth, 16; the tenth, 1024; the twentieth, 1,048,576; the thirtieth, 1,073,741,824; and the thirty-first, 2,147,483,648. In other words, if we raise two to the thirtieth power, we have 1,073,741,824; or to the thirty-first power, 2,147,483,648. Therefore, it is evident even to the school boy, that, to have the present population of the globe, the net population must be doubled more than thirty times and less than thirty-one times. By logarithms, we find it to be 30.75 times. After all allowances are made for natural deaths, wars, catastrophes, and losses of all kinds, if the human race would double its numbers 30.75 times, we would have the present population of the globe.
>
> Now, according to the chronology of Hales, based on the Septuagint text, 5077 years have elapsed since the flood, and 5177 years since the ancestors of mankind numbered only two, Noah and his wife. By dividing 5177 by 30.75, we find it requires an average of 168.3 years for the human race to double its numbers, in order to make the present population. This is a reasonable average length of time.
>
> Moreover, it is singularly confirmed by the number of Jews, or descendants of Jacob. According to Hales, 3850 years have passed since the marriage of Jacob. By the same method of calculation as above, the Jews, who, according to the Jewish yearbook for 1922, number 15,393,815, must have doubled their numbers 23.8758 times, or once every 161.251 years. The whole human race, therefore, on an average has doubled its numbers every 168.3 years; and the Jews, every 161.251 years. What a marvelous agreement!

So far so good. Leaving Dr. Williams' calculations to one side for a moment and making some of our own, it is a fact that between 1650 and 1920 (= 270 years) the population of the world increased about 3.7 times. In other words, during this period of reasonably reliable estimates of world population it has doubled at the rate of once in approximately 146 years. This is a figure of at least roughly the same

order of magnitude as Dr. Williams' more pious ones. A calculating astronomer practicing his own trade would regard it, all things considered, as about equivalent to close agreement.

Let us now return to the reverend gentleman's arithmetic, which we personally believe to have been inspired by the Prince of Darkness and not by God, as Dr. Williams thinks:

> Now the evolutionists claim that the human race is 2,000,000 years old. There is no good reason for believing that, during all these years the developing dominant species would not increase as rapidly as the Jews, or the human race in historic times, especially since the restraints of civilization and marriage did not exist. But let us generously suppose that these remote ancestors, beginning with one pair, doubled their numbers in 1612.51 years, one-tenth as rapidly as the Jews, or 1240 times in 2,000,000 years. If we raise 2 to the 1240th power, the result is 18,932,139,737,991 with 360 figures following. The population of the world therefore, would have been 18,932,139,737,991 decillion, decillion, decillion, decillion, decillion, decillion, decillion, decillion, decillion, decillion; or 18,932,139,737,991 vigintillion, vigintillion, vigintillion, vigintillion, vigintillion, vigintillion.
>
> Or, let us suppose that man, the dominant species, originated from a single pair, only 100,000 years ago, the shortest period suggested by any evolutionist (and much too short for evolution) and that the population doubled in 1612.51 years, one-tenth the Jewish rate of net increase, a most generous estimate. The present population of the globe should be 4,660,210,253,138,204,300 or 2,527,570,733 for every man, woman and child!

This is intended by Dr. Williams to make the evolutionist stop and think. But he has still more heavy artillery. What of this:

> Now, if there had been no flood to destroy the human race, then the descendants of Adam, in the 7333 years, would have been 16,384 times the 1,804,187,000, or 29,559,799,808,000; or computed at the Jewish rate of net increase for 7333 years since Adam, the population would have been still greater, or 35,184,372,088,832. These calculations are in perfect accord with the Scripture story of the special creation of man, and the destruction of the race by a flood. Had it not been for the flood, the earth could not have sustained the descendants of Adam. Is not this a demonstration, decisive and final?

Here we stop. There is a great deal more that might be said about this book, but all that we care to do in this review is to expose the Reverend Doctor's technique in the hope that it will whet the reader's appetite. He has corresponded with a good many of the doughtiest Anti-fundamentalist warriors and the quotations he prints from their letters make highly amusing reading. Why *do* people write silly answers to idiotic letters?

We want to close this review with a serious word. The numerical consequences of any theory of organic evolution, in respect of practically any particular whatever, have never been seriously or exhaustively studied by a competent mathematician. Such exceptions to this statement as are furnished by the work of Karl Pearson and J. B. S. Haldane, and a few others, fine as they are within their limitations, are trivial in comparison with the vastness of the problem really involved. Until adequate research along these lines has proceeded much farther than it has now, and until many more biologists are able than now are to comprehend what the problem really means, and to read intelligently contributions towards its solution, it is to be expected that we shall be confronted from time to time with theological arithmetic of the sort assembled in this book. *But*, in our humble opinion, it will be poor tactics on the part of scientific men to attempt to meet such cases by calling the authors names, or by brushing the matter lightly aside as misguided nonsense. For the truth is that any theory of evolution *does have* necessary numerical consequences, and until we know better than we now do just what these are for any particular

theory of evolution we happen at the time to be enamored of, it would seem the part of wisdom to be cautious in our handling of the other fellow's computations.

EMERGENT EVOLUTION AND THE SOCIAL.
By William Morton Wheeler.
Kegan Paul, Trench, Trubner and Co., Ltd.
2s. 6d. $3\frac{3}{4}$ x 6; 57 *London*

EMERGENT EVOLUTION AND THE DEVELOPMENT OF SOCIETIES.
By William Morton Wheeler.
W. W. Morton and Co., Inc.
$1.00 $4\frac{1}{4}$ x $6\frac{1}{2}$; 80 *New York*

These are the English and American editions respectively of a notable little book, which begins with Professor Wheeler's address given before the International Congress of Philosophy. The main idea is that when previously separate, distinct, and self-contained things combine together, the "whole" which emerges is usually something quite different from the mere sum of the things which combine to make it. For example, a person with the most extensive knowledge conceivable about hydrogen and oxygen alone could not possibly have predicted in advance of the trial that the result of combining two parts of the former gas with one of the latter would be that remarkable and useful substance, water, which is not a gas at all but a liquid—an obviously different kind of thing. Water, in short, is an emergent, something new and different. So also is a colony of ants, or bees, or the Republican National Committee. What such groups do, as wholes, is often or always quite different from what could be predicted by mere summation of the separate behaviors of their individual members.

The most important emergent levels in the course of evolution are usually listed in ascending order as space-time, matter, life, mind, and deity. Professor Wheeler thinks, in view of the "profuse and unabated emergence of idiots, morons, lunatics, criminals, and parasites in our midst," the prospect of the emergence of deity is "about as imminent as the Greek Kalends." He elaborates with great plausibility the idea that an important emergent level next in ascending order above mind is the social. Societies he regards as super-organisms. They behave in purposeful ways as wholes.

Not only is this brilliant little book valuable on account of its contribution to the theory of society, but it also gives a clearer picture to the general reader of the content and significance of the whole doctrine of emergent evolution than any other book of anything like the same brevity that has yet appeared.

THE SPECIES PROBLEM. *An Introduction to the Study of Evolutionary Divergence in Natural Populations.*
By G. C. Robson. *Oliver and Boyd*
15 shillings net *Edinburgh*
$5\frac{1}{2}$ x $8\frac{3}{4}$; vii + 283

An extremely interesting and valuable discussion of evolution written by a systematist and field naturalist. Of late years it has been chiefly the laboratory geneticist and the paleontologist who have discussed the subject, and it is therefore refreshing to hear talk about the origin of species by one whose professional business it is to deal with them at first hand on a large scale. The first chapter is devoted to a discussion of the various criteria which have been used to distinguish species. It is shown that none of these is completely satisfactory, and that the different ones fail to coincide completely in the results to which they lead.

The following topics are then taken up: The constitution of species and natural populations; physiological differentiation; the distribution of allied species; isolation as a factor in the divergence of species; the origin and spread of variant characters; correlation and the origin of groups. There is a bibliography covering 19 pages.

This book is a contribution of first-rate significance to the literature of evolution.

PALAEOBIOLOGICA.
Edited by Othenio Abel (with collaboration of Fritz Drevermann, Otto Jaekel, Franz Baron Nopcsa, and Jan Versluys.)
Emil Haim and Co.
50 marks (paper) *Wien*
53 marks (cloth)
6¾ x 9¾; iv + 376

A *Festschrift* in honor of Louis Dollo, on the completion of his seventieth year of life. It contains 28 papers on a wide variety of subjects in the general fields of palaeontology, comparative anatomy, and evolution, by distinguished workers on these subjects in various parts of the world. The volume is beautifully printed and illustrated, and does great credit to the publisher as well as to the editor. This *Festschrift* constitutes the first four parts of the first volume of a new journal to be devoted to palaeontology.

GENETICS

DIE ERGEBNISSE DER GENETISCHEN WEIZENFORSCHUNG.
By Birger Kajanus. *Martinus Nijhoff*
5 guilders *The Hague*
6¾ x 9⅝; 104 (paper)

This monograph, published in *Bibliographica Genetica* (III, 1927), reviews the literature on the genetics of wheat up to, and including, the year 1924. There is a bibliography of 214 titles.

HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Lieferung 1. Band III.* Containing following articles: *Entwicklungsmechanik und Vererbung bei Tieren*, by *W. Schleip*, and *Partielle Keimesschädigungen durch Radium und Röntgenstrahlen*, by *P. Hertwig.*
Gebrüder Borntraeger
9.60 marks 7 x 10½; 129 (paper) *Berlin*

Since the beginning of this century genetics has reached one of the first places among the branches of biological science. The tremendous growth of genetic literature published in all parts of the world, not only in special journals but in general biological and scientific periodicals, will soon make it really impossible for the average biologist to keep in touch with the progress in the different special lines of this subject. Textbooks on heredity have not the proper dimensions to fulfill this requirement.

The purpose of the *Handbuch* planned by Professors Baur and Hartmann is to review the whole field of modern genetics. Up to the present time no such work has been attempted. The material will be divided according to special problems and not according to groups of animals and plants, as was done by Lang (*Die experimentelle Vererbungslehre in der Zoölogie seit 1900*), and by several authors in the well-known *Bibliographia Genetica*.

The three volumes of the *Handbuch* will be made up of thirty-three sections, by twenty-nine collaborators, most of whom are well known German biologists, although the names of H. J. Muller (U. S. A.), J. Nilsson-Ehle (Sweden), and H. Federley (Finland) are included in the list.

The content of the *Handbuch* is broader than the title implies. The last volume will contain sections on evolution, the phylogeny of animals and plants, and the origin of domesticated animals and plants. A number of sections will be devoted to the applications of genetics: eugenics, and plant and animal breeding. When finished the *Handbuch* will be an indispensable reference book in the libraries of university biological laboratories, experiment stations, and individual workers in the fields of human, animal, and plant heredity.

The first section, now published, presents an attempt to connect the modern science of heredity with *Entwicklungsmechanik*—the physiology of development. It must be admitted that there is an obvious difficulty in correlating the two lines of investigation: the highly developed genetic theory, which permits us to predict with a very great degree of accuracy the characteristics of progeny in our hybridization experiments, on the one hand, and, on the other, an understanding of the mechanism by which the genes control the development of a growing organism.

The second part, written by Dr. Paula Hertwig, discusses one of the most interesting problems of present day genetics. It deals not only with the influence of radium and Röntgen rays, as may be learned from the title, upon the germ cells, but includes also a short review of experiments with other agencies. It should be noted that the discussion of the latter is far from complete. For instance, the well-known, although not entirely conclusive, temperature experiments of Standfuss, Fischer, etc., are not even mentioned. We should also prefer not to use the term "*Keimesschädigungen*" in describing the experiments on the influence of external agencies upon the germ cells, because it implies a certain amount of subjective judgment of the harmfulness of the effect. A neutral term *Keimesbeeinflussungen*, would be preferable.

ENTSTEHUNG DER HAUSTIERE. *Handbuch der Vererbungswissenschaft. Lieferung 2 (III, K)*
By B. Klatt. *Gebrüder Borntraeger*
15 marks 7 x 10½; 107 (paper) *Berlin*

This number of the Baur-Hartmann *Handbuch* is devoted to a thorough discussion, well illustrated, of the origin of the common domesticated animals, and of the modifying effects of domestication upon their structures and functions. There is a bibliography of eight pages.

THE PROSPECTIVE DEVELOPMENT OF PERU AS A SHEEP-BREEDING AND WOOL-GROWING COUNTRY.
By Aldred F. Barker. *Granja Modelo Puno Chuquibambilla, Peru*
7⅛ x 9⅞; xii + 174 (paper)

A report to the Peruvian government, by the Professor of textile industries at Leeds, which is of considerable interest and value to students of the genetics of sheep and wool.

GENERAL BIOLOGY

LA CONQUÊTE DE LA VIE.
By Serge Voronoff. *Eugène Fasquelle*
12 francs 4¾ x 7½; 228 (paper) *Paris*

In his latest volume Dr. Voronoff says about the same thing over again about his rejuvenation technique. We like the author's ideal, even if we are sceptical about its realization through testicular transplantation: "L'idéal vers lequel tendent nos efforts, c'est de conserver la vie

dans la plénitude de ses manifestations physiques et intellectuelles, d'abréger le temps de la vieillesse, et de reculer la mort à ses dernières limites. VIVRE JEUNE!"

In connection with Dr. Voronoff's work the readers of THE QUARTERLY REVIEW OF BIOLOGY will be interested in the report of an official investigation, recently issued by the Board of Agriculture for Scotland, on his animal experiments. A commission consisting of Dr. F. H. A. Marshall and Dr. A. Walton of Cambridge, and Dr. F. A. E. Crew and Mr. W. C. Miller of Edinburgh, went to the experimental farm in Algeria and studied the material in the experiments there under way. The commission was not satisfied that Dr. Voronoff had proved his thesis, either in the case of the rejuvenated bull or the grafted rams.

L'ORIGINE DE LA VIE. *La radiation et les êtres vivants.*
By Georges Lakhovsky.
Gauthier-Villars et Cie
20 francs $5\frac{1}{4} \times 7\frac{3}{4}$; 175 (paper) *Paris*

CONTRIBUTION À L'ÉTIOLOGIE DU CANCER.
By G. Lakhovsky. *Gauthier-Villars et Cie*
20 francs *Paris*
$9\frac{1}{2} \times 12\frac{3}{4}$; 12 + 4 plates (paper)

Dr. Lakhovsky's general idea is that the living cell is an elemental electric oscillator, which absorbs and emits electromagnetic radiations. Life is nothing other than the manifestation of this oscillatory state of the cell. In a state of health there is equilibrium between the waves absorbed and the waves emitted. Disease is electromagnetic disequilibration.

This will sound pretty dubious to the biologist generally speaking. But this is to be said; Dr. Lakhovsky is not one of those who speculates and lets it go at that, endeavoring merely to fortify the weakness of his case by the luxuriance of his verbosity. He researches, both by the experimental and the statistical route, and has brought to light in this way some curious things about cancer death rates, and plant cancers, in relation to cosmic rays, as he supposes. We direct particular attention to his most recent paper (at least to come to our attention) in the *Comptes Rendus*, 11 April, 1928. No experimentalist will be in the least convinced by the results there recounted, but perhaps the paper will stir some one up to repeat the experiments with some methodological precision. Also the curious correlations between cancer death rates and the character of the soil discussed in the second of the books here noted is interesting, but, alas, probably not significant.

A SHORTER PHYSICAL GEOGRAPHY.
By Emmanuel de Martonne. Translated from the French by E. D. Laborde.
Alfred A. Knopf, Inc.
$4.00 $5\frac{1}{2} \times 8\frac{3}{4}$; xvi + 338 *New York*

This book is primarily intended for teachers of physical geography, but the ecologists will find it useful in their work as a reference work, and for assigned collateral reading. Throughout the book the author, who is regarded as the leading exponent of physical geography in France, never loses sight of the fact that his subject is physical geography, and each phase is dealt with strictly from that point of view. He has judged to a nicety the amount of geology and physics necessary to build up geographical principles. Likewise, when he comes to the treatment of that part of the book dealing with plant and animal life his point of view is strictly geographical. At the end of each

general division of the book there is an appendix giving suggestions for further reading and for practical work demonstrating the important features under consideration. An excellent index adds to the usefulness of the book.

BIOLOGY OF THE VERTEBRATES.
A Comparative Study of Man and His Animal Allies.
By Herbert E. Walter. *The Macmillan Co.*
$5.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xxv + 788 *New York*

This excellent textbook is the outgrowth and embodiment of a course in vertebrate comparative anatomy which Professor Walter has taught for many years. It develops the subject along novel lines, and really justifies its main title. It is just as sound as the old Wiedershein text on which we were all nurtured a quarter of a century ago, and a great deal more interesting. Tastes will differ about the advisability of the occasionally journalistic diction and headlining in which the author has chosen to write. But after all this is only a matter of taste. The book is, regardless of its stylistic peculiarities, a valuable and original contribution to the elementary teaching literature of biology. There is only a short derivative bibliography, but the book is well indexed.

THE RATE OF LIVING. *Being an Account of some Experimental Studies on the Biology of Life Duration.*
By Raymond Pearl. *Alfred A. Knopf, Inc.*
$3.50 $5\frac{1}{2} \times 8$; v + 185 *New York*

This book, which embodies a series of lectures delivered at University College, London, summarizes and puts together in orderly fashion the results of the author's experimental studies on duration of life, carried out since 1920, with *Drosophila* and seedlings of *Cucumis melo* as the material chiefly used. Following introductory discussions of the history of the subject and the technique used in the experimental work, successive chapters deal with life tables for *Drosophila;* the effect of density of population on duration of life; the inheritance of longevity; inherent vitality; and the relation of total duration of life to the rate of vital activities. The general conclusion reached is that duration of life varies inversely as the rate of energy expenditure during its continuance. There is a bibliography of 141 titles.

DIE ÄTIOLOGIE DER BÖSARTIGEN GESCHWÜLSTE. *Nach dem gegenwärtigen Stande der klinischen Erfahrung und der experimentellen Forschung.*
By Carl Lewin. *Julius Springer*
18 marks *Berlin*
$6\frac{3}{4} \times 10\frac{1}{4}$; viii + 231 (paper)

A thorough, critical review of the work which has been done in the search for the cause of cancer. The author finds that the present status of investigation in this field does not warrant any final conclusion. There is a bibliography covering 24 pages. The general biologist will find this volume useful in orienting himself in regard to this vast experimental and clinical literature. Unfortunately there is no index.

ANIMAL BIOLOGY.
By J. B. S. Haldane and Julian Huxley.
Oxford University Press
$2.50 $4\frac{5}{8} \times 7\frac{3}{8}$; xvi + 344 *New York*

An elementary textbook of general biology which departs widely from the conventional, both in respect of emphasis and mode of treatment of the different subjects. As would be expected from the

senior author's predilections greater space and much more adequate treatment than is usual in textbooks fall to the functional as contrasted with the morphological aspects of general biology. It is a brilliantly written volume, which will find perhaps even greater usefulness as an introduction to the subject for the adult layman, than as a school textbook, though in the latter rôle its position is outstanding.

THE EFFECT OF AQUEOUS EXTRACTS OF TAR ON DEVELOPING TROUT OVA AND ON ALEVINS. *Fishery Investigations. Series I. Vol. III. No. 2.*
By A. C. Gardiner. *H. M. Stationery Office*
1s. 3d. $7\frac{1}{4} \times 10\frac{3}{4}$; 14 (paper) *London*

One volume of Road Board Tar was agitated for 18 hours with 3 volumes of water to form a stock solution. One part of stock solution to 10 volumes and to 50 volumes of water formed strong and dilute test solutions. The results showed that such tar extracts were wholly without effect upon ova and very young fry, but with advancing age the susceptibility to poisoning increases, so that fry 110–115 days old could not stand more than 15 minutes immersion in a solution of 40/100,000 phenol. Even so they had greater resistance than yearling trout.

DIE GEWEBEZÜCHTUNG IN VITRO.
By V. Bisceglie and A. Juhász-Schäffer.
Julius Springer
24 marks (paper) *Berlin*
25.40 marks (bound)
$5\frac{3}{4} \times 8\frac{3}{4}$; viii + 355

This useful treatise constitutes Volume 14 of the series of *Monographien aus dem Gesamtgebiet der Physiologie der Pflanzen und der Tiere.* It reviews the now extensive literature which exists on the technique and results of tissue culture *in vitro.* There are 71 illustrations, and an extensive bibliography, covering some 42 closely printed pages.

ÜBER DEN TOD.
By Georg Perthes. *Ferdinand Enke*
2.80 marks *Stuttgart*
$6\frac{1}{4} \times 9\frac{3}{8}$; 73 (paper)

The second edition of a pamphlet which contains two essays on the general subject of senescence and death. The first is a discussion of the manner of death. The second, which is a posthumous publication, deals with the general biology of death.

INDEX BIOLOGORUM. *Investigatores. Laboratoria. Periodica.*
Edited by G. Chr. Hirsch. *Julius Springer*
27 marks $5\frac{3}{4} \times 8\frac{1}{2}$; vi + 545 *Berlin*

This is an extraordinarily useful and well-edited international Who's Who of workers in the biological sciences. It seems rather expensive, considering its size and the considerable sale which it is sure to have, but it is well worth the money as a clerical assistant in any laboratory or library. The sub-title indicates its scope.

DE LAMAR LECTURES 1926–1927. *The Johns Hopkins University, School of Hygiene and Public Health.*
The Williams & Wilkins Co.
$5.00 6 x 9; 223 *Baltimore*

These lectures are chiefly of interest to the public health worker and the medical man. But one will be welcomed by the general biologist. Dr. G. H. F. Nuttall, Quick professor of biology in the University of Cambridge, discourses in a most

entertaining manner about "Some pioneers in parasitology."

HUMAN BIOLOGY

THE AMERICAN NEGRO. *A Study in Racial Crossing.*
By Melville J. Herskovits.
Alfred A. Knopf, Inc.
$1.75 5 x 7½; xiv + 92 *New York*

This little book furnishes an excellent summary, in readable form comprehensible to the lay reader, of the results of the important studies that Dr. Herskovits has been making during the past four or five years on the anthropology of the American negro. The work has been carefully and thoroughly done, and therefore the conclusions reached are worthy of serious consideration. They run counter to a whole flock of preconceptions of geneticists and eugenists. Let it first be noted that Dr. Herskovits has worked with "run-of-mine" negroes, chiefly in Washington, D. C., in respect of whom it is idle to talk about "pure" negroes, or "first crosses" between white and negro. "The population we have considered is not the first nor even the second filial generation, in the main, but is farther removed from the original crossing."

Now for the results.

> What we see is that in trait after trait the average is about half-way between the averages for the White population and the African, so that what we have represented here is a blend, if the gross statistical analysis is correct. In the second place there would have to be an increase in variability if the Mendelian hypothesis were operative in this case. But I need not repeat the fact that the American Negro is homogeneous, and that the index of this homogeneity is the low variability of trait after trait when this variability is compared with that of the so-called "pure" populations. Results such as these must give us pause. It may be that Mendelian heredity is operating in a way so complex that it cannot be discerned by the use of statistical analysis of adult groups, although this type of material constitutes by far the greatest portion of that available. When the actual heredity from parents to children is investigated, a new light may be thrown on the situation. But the data which have gone into this study of the American Negro thus far do not seem, when analyzed, to show any tendency to act according to the requirements of the Mendelian hypothesis.

We heartily commend this entertaining and significant little volume to our readers.

A STUDY OF RACES IN THE ANCIENT NEAR EAST.
By William H. Worrell.
D. Appleton and Co.
$3.00 5⅜ x 8⅛; xiv + 139 *New York*

In brief space the author of this interesting volume, who is Associate Professor of Semitics in the University of Michigan, brings to bear geographic, ethnologic, and linguistic evidence upon the problem of the disentanglement of the knotty skein of race in the Near East. At the start he states that the book is the outcome of a

> life-long romantic interest in race, which has been fed and deepened by long contact with the Jewish people of many lands. They are The Race. As I stand before these faces, representing many types, I fancy I see in real presence Hittite and Babylonian, Canaanite and Aramaean; now all "Jews," many American citizens, some eminent in modern life, speaking the Germanic-Romance language of the British Isles, or the medieval German of the Rhineland, or the Spagnoli and Arabic of Moorish Spain. Once, I know, their forebears wrote works in Arabic, and before that in Hellenistic Greek and Aramaic, and before that in Hebrew. They came out of Arabia, the fountain-head of Semitic speech. Behind the intricacies and mysteries of Arabic lie the revelations of ancient Akkadian and Ethiopic. But this is only the beginning: The pictured monuments of Egypt tell us that the most archaic Semitic speech is no more than an early offshoot of a trunk whose branches even now flourish all over Africa. With this type of speech there went a race which by degrees we trace back to the Atlas highlands. We

fancy we can almost follow them across into Europe, and imagine them the builders of Stonehenge and the dolmens of Brittany. Perhaps they were the people of Druidism. It may be that Caesar's soldiers heard in Aquitania the last echoes of European Hamitic speech; and that Goidels and Brythons learned from Pictish mothers the idioms of this pre-Aryan British tongue. And may not this have been indeed, the language of the whole Mediterranean race?

The book includes a number of excellently chosen photographs of racial types. Altogether it is a valuable addition to the literature on a particularly puzzling problem in the biology of human races.

HEREDITY AND HUMAN AFFAIRS.
By Edward M. East. Charles Scribner's Sons
$3.50 6 x 8¾; vii + 325 *New York*

This book is, without doubt, the best presentation of the eugenic position that has yet been prepared for the general reader. Professor East has all the requisites for producing such a book; a commanding position among scientific students of genetics; a wide knowledge of human biology; and the ability to write with clarity and vigor.

The wide scope of the book is indicated by the chapter headings: Science and the new era of humanism; heredity—late master riddle of science; the machinery of heredity; the grammar of heredity; heredity and sex; the inheritance of human types; the two collaborators—heredity and environment; marriage between near kin; racial traits; some specific race problems; genius, mediocrity, and education; the lower levels of humanity; the survival of the underman; immigration; the problems of every-day life.

There is thorough documentation throughout. The writer of this notice does not agree with Professor East's position on a number of eugenic matters, and probably there are other biologists who do not. But this is a point of no particular consequence. The important thing is that in this book we have a competent, authoritative, well written exposition of the present status of eugenic science, which will not only inform the public but also be of great help to every worker in this field as a reference source.

ACCRESCIMENTO CORPOREO E COSTITUZIONI DELL'UOMO.
By Luigi Castaldi. Luigi Niccolai
50 lire *Florence*
6⅞ x 9¾; viii + 350 (paper)

This is a contribution to human biology in general, and to constitutional morphology in particular, of real interest and importance. In several respects it must be regarded as a model for scientific investigation in the field of constitutional morphology, however much any particular reader may be inclined to disagree with particular details. The literature is extensively and intelligently reviewed as a background to the author's own researches on human growth. The scope of the book is indicated by the following list of the main divisions of the treatment: Definition of body growth; methods for the biometrical study of growth; prenatal growth of the body as a whole and of the principal viscera; postnatal growth of the body as a whole; postnatal growth of the principal viscera; the results of growth as expressed in ideal types, and in constitutional morphological types; the growth of cells and tissues; causal factors in the corporeal growth of man (endocrines, etc.); anomalies and disharmonies of growth; some eugenic considerations.

The book is very well indexed and abundantly illustrated. We heartily commend it to our readers as a stimulating and interesting contribution.

FOOTPRINTS OF EARLY MAN.
By Donald A. Mackenzie.
Blackie and Son, Ltd.
5 shillings *Glasgow*
$5\frac{1}{4} \times 7\frac{3}{8}$; xviii + 190

In this readable, if not very deep, book the author has brought together brief descriptions of all of the more important records that have been left by ancient man. Sand and gravel pits, asphalt beds and caves have furnished contributions to our knowledge of prehistory. Based upon these discoveries the author reconstructs what he conceives to be the customs, modes of living and wanderings of primitive man. The narrative is brought down to the dawn of what we still oddly call the "historical" period. Summaries are given of the archeological finds made by recent expeditions to China and the Gobi Desert, as well as descriptions of the recent discoveries of the Galilee, Rhodesian and "Lady of Lloyds" skulls.

This book, being in no way technical, will be of interest to the general reader. The volume is illustrated by 16 plates, and a brief bibliography of one page is given, containing a list of the chief works of reference consulted by the writer.

THE RACIAL ELEMENTS OF EUROPEAN HISTORY.
By Hans F. K. Günther (Translated from the second German edition by G. C. Wheeler).
E. P. Dutton and Co.
\$4.60 $5\frac{1}{2} \times 8\frac{3}{4}$; vi + 279 *New York*

The early chapters of this book deal with an analysis of the population of Europe into five distinct types or races. The analysis is made chiefly by means of anthropometric measurements, but mental traits are likewise considered. Much stress is put upon the importance of the correlation of certain characteristics in obtaining a true picture of the several races making up a population. Considerable space is devoted to the European races (particularly the Nordic) in prehistory and history, the author's main thesis being that "When we survey the fall in each case of the great empires and creative cultures from India to the West, this much is always clearly to be seen: that every 'fall' of a people of Indo-European speech is brought about through the running dry of the blood of the creative, the Nordic race."

In the concluding chapters the author discusses the position of the Nordics at the present time—not only in Europe but in America as well—pointing out the dangers that beset this strain of the human race, which the author regards as particularly valuable.

There are numerous illustrations, which assist the reader to a better understanding of the comparisons which the author makes between the different races. The book as a whole is a piece of Nordic propaganda, reasonably sound on the somatological side, but much more dubious when it goes over into the fields of history and race psychology.

A SURVEY OF THE SOCIAL STRUCTURE OF ENGLAND AND WALES *as Illustrated by Statistics.*
By A. M. Carr-Saunders and D. Caradog Jones. *Oxford University Press*
10 shillings *London*
$5\frac{1}{2} \times 8\frac{1}{2}$; xvii + 246

An admirable attempt to recover the dry bones of social statistics with flesh, to reconstruct from the data of the Census and other statistical sources the organism called English society. Starting with an analysis of the population by age and sex the authors are led to an examination of

marital condition, family groups, housing, urbanization and geographical distribution of the population, industry, occupation, industrial status, trade unions and professional associations, political, social, and religious associations, the national income and its distribution, the national wealth, education, entrance into occupations, state provision against misfortune and its effect on the distribution of the national income, voluntary provision against misfortune, charities, poverty, crime, and the inborn qualities and recruitment of the population. The reader unversed in statistics will have a new idea when he finishes the book of how illuminating the statistical treatment of a subject may be. The discussions of official terminology are sometimes diverting. Thus the definition of a rural district as "one under a rural district council" is reminiscent of Sydney Smith's definition of an archdeacon as "a person performing archidiaconal functions." There is an appendix giving the sources of information but no index.

EPIDEMIC INFLUENZA. *A Survey.*
By Edwin O. Jordan.
American Medical Assoc.
$5.00 $5\frac{3}{8}$ x $8\frac{1}{2}$; 599 *Chicago*

This treatise is destined to be of great and permanent value as a document in the history of epidemiology. For it is a thorough, sound, critical and comprehensive digest of all that is known about the great pandemic of influenza which occurred with such devastating results in 1918. Probably no one was so well qualified to undertake this difficult task as Professor Jordan, both because of his wide-ranging knowledge and experience in epidemiology, and his calm and critical judgment. The book is of value not alone to the professional epidemiologist; the student of human biology in general will find in it much that is suggestive and useful to him. There is a bibliography covering 52 pages, and detailed author and subject indices.

NEGRO PROBLEMS IN CITIES. *A Study made under the direction of T. J. Woofter, Jr.*
Doubleday, Doran and Co., Inc.
$2.50 net *Garden City, N. Y.*
5 x $7\frac{1}{2}$; 285

The rapid increase of the negro population in American cities, from 750,000 in 1870, to 2,000,000 in 1900, and 4,000,000 in 1925, justifies a thorough survey of the environmental factors which affect the negro, and his reactions to them. This survey, made by the Institute of Social and Religious Research, gives the results of studies made in seven northern and nine southern cities. It is concerned chiefly with housing, schools, and recreations of the negro and negro neighborhoods. A staff of four people, two white and two colored, investigated conditions in these cities, and with the aid of local individuals and organizations amassed considerable pertinent information bearing upon the negro problem.

MAX VON PETTENKOFER. *His Theory of the Etiology of Cholera, Typhoid Fever and Other Intestinal Diseases. A Review of His Arguments and Evidence.*
By Edgar E. Hume. *Paul B. Hoeber, Inc.*
$1.50 net 5 x $7\frac{1}{2}$; xv + 142 *New York*

Dr. Hume has done a real service to epidemiology and preventive medicine, and to human biology generally by resurrecting Pettenkofer's work from the oblivion into which it had almost com-

pletely fallen. Max von Pettenkofer was a great man, who paid a heavy penalty for having lived at the same time that Pasteur did. Even to this day it is impossible for any sort of bacteriological work relating to disease to get consideration strictly and solely on its objective merits. All such work is evaluated, consciously or unconsciously, on the basis of dicta laid down by Pasteur and Koch. Pettenkofer's theories of epidemics fared badly under such Procrustean limitations. Hume says that his hypothesis is "no longer tenable." But is there any general theory of epidemiology today which pretends that it includes all the variables which are important in the production of epidemics?

Dr. Hume has written an extremely interesting and valuable little book. There is a bibliography of 285 titles.

AUTOUR DES INSCRIPTIONS DE GLOZEL.
By René Dussaud. *Armand Colin*
5 francs 5¼ x 8; 57 (paper) *Paris*

The Glozel controversy has become the leading topic of conversation wherever anthropologists and archaeologists are gathered. The French workers in these fields are apparently irreconcilably divided on the matter. The official report, and the writings of independent investigators who have studied the *corpus delicti* on the spot, serve apparently only to widen the breach, instead of bringing the contending parties together.

In the present pamphlet the author, who is a member of the Institute, an assistant curator of the Louvre, and a specialist on Semitic inscriptions, comes to the conclusion that all the inscriptions on the famous tablets alleged to have been excavated at Glozel are fakes, pure and simple.

NATURAL MAN. *A Record from Borneo.*
By Charles Hose. *The Macmillan Co.*
$10.00 6¾ x 9¾; xvi + 284 *New York*

Sir Charles Hose has been for many years an administrative officer in Borneo. He collaborated with Professor William McDougall in writing *The Pagan Tribes of Borneo*, and has aided with material comparative anatomists and anthropologists all over the world. This book is based on his long personal acquaintance with the various native tribes of Borneo, and contains a wealth of material of great value to the student of cultural evolution. Of particular interest is his account of the Punans, a tribe which has practically no culture whatever. These people are, in some sense, cultural fossils, comparable in their significance for the study of cultural evolution to that of *Archaeopterx* in the study of comparative anatomy. The book is interestingly written, and well indexed. Professor Elliot Smith contributes an introduction.

MAYA CITIES. *A Record of Exploration and Adventure in Middle America.*
By Thomas Gann. *Charles Scribner's Sons*
$5.00 5¾ x 9; 256 *New York*

The author, who is an experienced traveller and explorer, entertainingly describes his most recent discoveries and adventures in British Honduras. Besides being of importance archeologically, the book is charmingly written. Numerous illustrations give it added interest. The author incidentally records a good many interesting and new observations on the plant and animal life of the region. Perhaps the outstanding feature of the book is the picture it gives of the still unexploited opportunities for discoveries in British Honduras regarding the Maya and earlier civilizations.

LE NON-CIVILISÉ ET NOUS. *Différence Irréductible ou Identité Foncière?*
By Raoul Allier. *Payot*
25 francs $5\frac{5}{8} \times 9$; 317 (paper) *Paris*

This is an analysis of the primitive mind, starting from the basic question as to whether there are two fundamentally different kinds of human beings—one capable of making all the progress and the other destined merely to serve the former or perish. The conclusion is that, at bottom, all human beings have a good deal in common, although some have been the victims of a knotty entanglement psychically which seems to have permanently arrested all possibility of any new development. The bearing of all this on the problem of colonization is one of the chief concerns of an interesting book.

LA FRANCE ET LES ÉTRANGERS (*Dépopulation. Immigration. Naturalisation*).
By Charles Lambert. *Librairie Delagrave*
7 francs $4\frac{3}{4} \times 7\frac{3}{8}$; 155 (paper) *Paris*

Although at bottom a piece of political propaganda, with an introduction contributed by M. Herriot, this little volume will be a useful addition to the library shelves of the human biologist interested in the problem of migration. Since the war France has had such a large immigration that the thoughtful among her citizens are beginning to be disturbed over its present and potential consequences. This book is a discussion of the facts, and of what is to be done about them.

LA QUESTION DU LAIT. *Étude Médicale, Biologique et Sociale.*
By J. Rennes. *Masson et Cie*
18 francs $6 \times 9\frac{1}{8}$; 222 (paper) *Paris*

Those in this country who have struggled to secure clean and wholesome milk will doubtless be interested in this account of the problem as it presents itself in France. The author discusses first, the factors that affect the goodness and badness of milk; second, the political and psychologic factors involved in the campaign for better conditions; and third, the psychology of the milk man and the methods to be used in teaching him and in controlling his behavior.

STAMMBAUM UND ARTBILD DER DEUTSCHEN UND IHRER VERWANDTEN. *Ein kultur- und rassengeschichtlicher Versuch.*
By Fritz Kern. *J. F. Lehmanns Verlag*
13 marks (paper) *München*
15 marks (bound)
$6 \times 8\frac{3}{4}$; viii + 305

The general conclusion of this semi-popular treatise, with 445 illustrations, which discusses the evolutionary ancestry of the German people, is that what has hitherto been regarded as the pure Nordic race is probably a composite of two races—one the descendants of Cromagnon man, the other the true Nordic race. In present day Germans are to be seen both races in close combination and more or less complete fusion.

ABRISS DER ERBBIOLOGIE UND EUGENIK.
By R. Fetscher. *Otto Salle*
4 marks $5\frac{1}{2} \times 7\frac{5}{8}$; viii + 155 *Berlin*

An excellent little popular treatise on human inheritance and eugenics, constituting Volume 10 of a series with the general title "*Mathematisch-naturwissenschaftlich-technische Bücherei.*" There are 79 illustrations, and a brief bibliography of the more important German books on the subjects treated.

RASSENKUNDE DES DEUTSCHEN VOLKES.
By Hans F. R. Günther.
J. F. Lehmanns Verlag
12 marks (paper) *München*
14 marks (bound)
$5\frac{3}{4}$ x 9; viii + 498

The twelfth edition of a popular treatise on the race biology of the German people. It is extensively and well illustrated, and on this account, chiefly, valuable as a reference book for students of human biology generally. The significance of the Nordics in the general scheme of things is not underemphasized.

THE SEARCH FOR ATLANTIS. *Excursions by a Layman Among Old Legends and New Discoveries.*
By Edwin Björkman. *Alfred A. Knopf, Inc.*
$2.00 5 x $7\frac{1}{2}$; 119 *New York*

A theory concerning Atlantis. The author, who is not primarily an archaeologist, has delved with enthusiasm into classical legends and modern archaeology and from this study has produced a book which the general reader will find of interest. He links Atlantis with the Island of Scheria, the home of Nausicaä, and also with the ancient city of Tarshish, sister city to Glades (modern Cadiz).

RASSENFORSCHUNG. *Eine Einführung in rassenkundliche Methoden.*
By Walter Scheidt. *Georg Thieme*
5.80 marks $6\frac{1}{2}$ x $9\frac{1}{4}$; 82 (paper) *Leipzig*

A useful little handbook of anthropometric technique and statistical methods, which will be particularly interesting to students of constitutional medicine, as well as to anthropologists.

MORTALITY AMONG NEGROES IN THE UNITED STATES. *Public Health Bulletin No. 174.*
By Mary Gover.
U. S. Government Printing Office
15 cents *Washington, D. C.*
$5\frac{7}{8}$ x $9\frac{1}{4}$; vi + 63 (paper)

A thorough and valuable study of the mortality statistics of negroes in comparison with whites. It will be found useful by all students of human biology.

ZOOLOGY

LES ÉLATÉRIDES DE L'INDO-CHINE FRANÇAISE.
By F. Fleutiaux.
25 francs $6\frac{3}{4}$ x 10; 71 (paper)

THERMOSBÆNA MIRABILIS MONOD. *Remarques sur sa morphologie et sa position systématique.*
By Th. Monod.
8 francs $6\frac{3}{4}$ x 10; 30 (paper)

CONTRIBUTION À L'ÉTUDE SYSTÉMATIQUE ET BIOLOGIQUE DES TERMITES DE L'INDOCHINE.
By Jean Bathellier.
80 francs $6\frac{3}{4}$ x 10; 240 (paper)

LES GALLINACÉS ET PIGEONS DE L'ANNAM.
By J. Delacour and P. Jabouille.
Société d'Éditions Géographiques, Maritimes et Coloniales
40 francs $6\frac{3}{4}$ x 10; 92 (paper) *Paris*

These four pamphlets, all published in 1927, are parts of the first volume of a noteworthy zoological enterprise, the *Faune des Colonies Françaises*, undertaken by the indicated publisher, under the general editorial direction of Professor Gruvel, and the patronage of the Colonial Ministry, the Academy of Sciences, the Pasteur Institute, and a number of other similarly important bodies.

The first fascicle noted is a purely taxonomic list of the elaterid beetles of French Indo-China.

The second discusses the morphology of the extraordinary thermophile crustacean discovered in Tunisia and described by Monod in 1924. He now shows that it is an adult form, and creates for it a new order, the Thermosbaenacea, lying between the Mysidacea and the Tanaidacea.

The third fascicle is an important contribution to the general biology of the termites, dealing successively with a systematic catalogue of the species of termites found in Indo-China; observations on their habits, habitations, means of defense, etc.; their development and the determination of castes; and finally the cultivation of mycelia by the termites of Indo-China. The treatise is extensively and well illustrated and concludes with a bibliography covering five pages.

The last of these four fascicles is a taxonomic review of the Phasianidae, Turnicidae, and Columbae of Annam, fully illustrated by text figures and plates, many of the latter being colored.

To this worthy enterprise, the *Faune des Colonies Françaises*, we wish all success.

NATURAL HISTORY: ANIMALS.
TABLE OF GESTATION PERIOD AND NUMBER OF YOUNG. *An Appendix to Natural History: Animals.*
By George Jennison. *A. and C. Black, Ltd.*
12s. 6d. $5\frac{3}{4} \times 8\frac{5}{8}$; xv + 344 *London*
Appendix 1 shilling
$5\frac{1}{2} \times 8\frac{1}{4}$; 8 (paper)
(Sold in United States by The Macmillan Co., New York, $4.50)

"An Illustrated Who's Who of the Animal World" is the sub-title given to this book by the author, late Curator of the Zoological Garden at Manchester. This dictionary of mammals has obviously been compiled with much care and labor. It should prove a valuable book for identification purposes, since by its numerous illustrations and detailed descriptions easy recognition of a considerable number of genera and species is possible. There are over 300 photographic illustrations, and 16 full page illustrations in color.

The descriptions pay especial attention to size and external form. Certain special features, such as the curiously different markings of predatory and peaceful animals, the longer life of caged creatures in countries other than their own, the expectation of life of a specimen caged in good health, also many historical references culled from old pictorial or written records, have been included in this interesting book. An extensive table on gestation periods (which may be obtained separately) is appended at the end of the book.

THE PLATYPUS. *Its Discovery, Zoological Position, Form and Characteristics, Habits, Life History, etc.*
By Harry Burrell.
Angus and Robertson, Ltd.
25s. (post 6 d.) *Sydney, Australia*
$5\frac{1}{2} \times 8\frac{5}{8}$; 227

This book is the outcome of nearly twenty years personal observation of *Ornithorhynchus paradoxus* in its natural haunts, carried out while the author was engaged in collecting for the University of Sydney. It is intended mainly for the general reader, but will be an extremely valuable addition to every biological laboratory where comparative anatomy and evolution are taught. It is illustrated with 35 plates in addition to text figures. The ground covered is as follows: Dis-

covery and early descriptions; controversy on the zoological position; controversy on the laying of eggs; general characteristics; nervous organization and sensory perceptions; the spur and crural gland; the nesting-burrow; distribution and haunts; habits; breeding habits and life history; preservation and economics; the platypus in captivity. There is a bibliography covering four pages of fine print.

We heartily recommend this book to everyone interested in natural history, from any angle whatever.

ANIMAL LIFE OF THE CARLSBAD CAVERN.

By Vernon Bailey.

The Williams & Wilkins Co.

$3.00 5¾ x 8; xiii + 195 *Baltimore*

Carlsbad Cavern, "the most extensive and spectacular cavern yet discovered in America if not in the world," in Southeastern New Mexico, was set aside as a National Monument by President Coolidge in 1923. The National Geographical Society has supported a thorough study of its geology, structure, formation and extent. To Dr. Vernon Bailey was entrusted the study of the animal life of the cavern. The present report he regards as a preliminary reconnaissance, to be followed by a more extensive work in the future. He writes chiefly of mammals, there being a paucity of invertebrate life, due largely to the lack of organic matter to serve as food for such forms. This book will be of especial interest to the naturalist, but the visitor to the caverns will do well to include it in his luggage in order to satisfy his curiosity should he develop the yearnings of a naturalist.

BIRDS AND BEASTS OF THE ROMAN ZOO. *Some observations of a Lover of Animals.*

By Th. Knottnerus-Meyer. Translated by Bernard Miall. *The Century Co.*

$4.00 5½ x 8⅛; vii + 378 *New York*

A very interesting account of the author's life-long experience with animals in zoological gardens, with particular reference to the garden in Rome, of which he is the director. Dr. Knottnerus-Meyer got his training in Germany, in the Hagenbeck tradition. The book is a mine of information for the student of animal behavior and psychology, entertainingly written and fully and well illustrated. Unfortunately there is no index.

PRÉCIS DE PARASITOLOGIE.

By E. Brumpt. *Masson et Cie*

100 francs 5¾ x 7½; viii + 1452 *Paris*

This is the fourth edition of what is generally considered to be the best book on parasitology in the French language. It contains 795 figures in the text and 5 plates, 2 of them colored. The third edition, which appeared in 1922 and consisted of 1216 pages, has been entirely rewritten. The book opens with an introduction of 54 pages on parasitism in general; this is followed by four sections,—346 pages on protozoa, 423 pages on parasitic worms, 321 pages on arthropods, and 258 pages on vegetable parasites, especially fungi. A chapter of 60 pages on the spirochaetes is included in the section on protozoa. In covering such an enormous field the author has set for himself a difficult task. He has, nevertheless, acquitted himself with credit. The subject matter is almost entirely devoted to parasites of man. Naturally the

author, who is himself a distinguished investigator in the several fields covered by the book, emphasizes his own particular views, a procedure that is not very satisfactory in a text-book. Another failing exhibited by the author is that of accepting without sufficient scepticism the results of certain other investigators, principally those of medical men who have had little or no training in parasitology. On the whole, however, the book gives an admirable survey of the subject of human parasitology.

THE PLANT LICE OR APHIDIDAE OF GREAT BRITAIN. *Vol. II.*
By Fred V. Theobald. *Headley Brothers*
30 shillings $5\frac{3}{4} \times 8\frac{3}{4}$; 411 (paper) *London*

This is the second volume of a monographic review of the Aphididae, the first volume of which was noticed earlier in these columns. This section of the work carries the discussion part way through the Tribe *Callipterini*. The descriptions are very thorough, not only in respect of morphology, but also of habits, host plants, general ecology, etc. The work when completed will be a standard reference work for a long time to come.

A SHORT ILLUSTRATED GUIDE TO THE ANOPHELINES OF TROPICAL AND SOUTH AFRICA.
By Alwen M. Evans.
University Press of Liverpool
7s. 6d. (paper) $7\frac{1}{4} \times 10\frac{1}{2}$; 79 *Liverpool*
9 shillings (cloth)

This compact but comprehensive survey of the anopheline mosquitoes of Africa south of the Sahara should be of great value to sanitary officers working in that continent. Keys for the identification of all adult anophelines and of some of the common larvae are included. Under each species the distinctive characteristics and variations of adults and larvae are briefly discussed, and the available information on habits, breeding places and pathogenicity is summarized. The ten text-figures are largely devoted to the delineation of larval details, while five beautifully executed half-tone plates present the color-patterns of wings, legs, palps, etc., very accurately and effectively. The six plates which reproduce photographs of various anopheline breeding places add little to the book and might well have been omitted.

MYSTERIES OF THE ZOO.
By Helen M. Sidebotham.
Cassell and Co., Ltd.
5 shillings net $4\frac{7}{8} \times 7\frac{1}{4}$; 192 *London*

This book gives a brief history of the birth and development of the London Zoo. In an entertaining manner are described the individual habits, the likes and dislikes and friendships of many of the famous animals that have made the Zoo one of the most fascinating places in London. The ten illustrations are well chosen.

ANIMAL ECOLOGY. *With Especial Reference to Insects.*
By Royal N. Chapman.
Burgess-Roseberry Co.
$6.00 *Minneapolis*
$8\frac{1}{4} \times 10\frac{3}{4}$; ix + 183 (paper)

This is the second edition of an elementary textbook of animal ecology, issued in mimeograph form, and embodying a course in the ecology of insects which the author has given at the University of Minnesota for nine years. The book is characterized by two highly valuable

features; first, the quantitative method of approach to ecological problems which is emphasized throughout, and, second, the extensive bibliographies. It is to be hoped that the author will feel willing to make it more widely and comfortably available in printed form before long, for it is an excellent book.

PHYSICAL OCEANOGRAPHY OF THE GULF OF MAINE. *Bulletin of the Bureau of Fisheries Vol. XL, Part II.*
By Henry B. Bigelow.
U. S. Government Printing Office
$1.50 *Washington, D. C.*
7½ x 11; 516 (paper)

This volume completes a general report on the oceanographic survey of the Gulf of Maine, which has been issued in three parts. The first was devoted to fishes (Bigelow and Welsh, 1925), and the second to Plankton (Bigelow, 1926). They have been noticed in earlier numbers of The Quarterly Review of Biology. In the preparation of the final memoir, in which the various physical features are treated with great detail, the author had the collaboration of R. Parmenter and E. H. Smith. A lengthy bibliography completes the volume.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung X.*
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft m.b.H.
16.80 marks 6 x 8½; 204 (paper) *Leipzig*

This number of the handbook of the fauna of the North and Baltic Seas, earlier parts of which have been noticed in these columns, contains three articles: Gastrotricha, by A. Remane; Halacaridae, by K. Viets; and Teleostei Physoclisti 11–15, by E. W. Mohr and G. Duncker.

MAMMALS AND BIRDS OF MOUNT RAINIER NATIONAL PARK.
By Walter P. Taylor and William T. Shaw.
U. S. Government Printing Office
85 cents *Washington, D. C.*
5¾ x 9⅛; viii + 249 (paper)

A handbook, prepared primarily for National Park visitors, but of much wider interest and usefulness. It should be in every zoological library as a reference work in vertebrate zoology, natural history, and ecology. The book is extensively and beautifully illustrated.

SAGITTA. *Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals.*
By S. T. Burfield.
The University Press of Liverpool, Ltd.
6s. 6d. *Liverpool*
6 x 9½; viii + 104 + 12 plates

This twenty-eighth number in the L. M. B. C. series of memoirs deals with the typical chaetognath. The morphology of *Sagitta* is described and illustrated in detail. This is followed by a short section on the embryonic development, and a bibliography of 109 titles.

BOTANY

PLANT AUTOGRAPHS AND THEIR REVELATIONS.
By Sir Jagadis Chunder Bose.
The Macmillan Co.
$2.50 5¼ x 7¾; xvi + 240 *New York*

This is stated to be the first book that Professor Bose has ever written for the lay reader. It is a popular summary, with numerous illustrations, of the results of his varied researches. It makes fascinatingly interesting reading. Unfortu-

nately there seems to be a good deal of doubt on the part of plant physiologists, within whose field most of the work falls, as to the soundness of some of the results, and particularly some of the conclusions.

FORESTS AND WATER IN THE LIGHT OF SCIENTIFIC INVESTIGATIONS.
By Raphael Zon.
U. S. Government Printing Office
20 cents *Washington, D. C.*
$5\frac{7}{8}$ x 9; 106 (paper)

This reprint from the Report of the National Waterways Commission, in which the author has sought to assemble all the well established scientific facts in regard to the relation of forest to water supply, will be of great value to the student of these problems. The statement of what is already definitely known serves to show where future problems lie. Of especial usefulness is the bibliography covering 36 pages at the end of the paper.

THE MARINE ALGÆ OF FLORIDA WITH SPECIAL REFERENCE TO THE DRY TORTUGAS. *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington. Volume XXV. Publication 379.*
By Wm. Randolph Taylor.
Carnegie Institution
\$3.00 (paper) *Washington, D. C.*
\$4.00 (cloth)
$8\frac{3}{4}$ x $11\frac{1}{4}$; 219 + 37 plates

A taxonomic treatise, thoroughly documented and illustrated, with notes on the ecological aspects of the algal flora of the Dry Tortugas.

LA SPORE DES CHAMPIGNONS SUPÉRIEURS. *Couleur. Forme. Ornementation. Terminologie. Valeur Taxonomique.*
By E. J. Gilbert. *Librairie E. le François*
20 francs $4\frac{3}{4}$ x $7\frac{1}{2}$; 221 (paper) *Paris*

This is the first volume of a proposed series *Les Livres du Mycologue.* It is a thorough discussion of the morphology of the spores of mushrooms, and their taxonomic significance. Its usefulness would have been greatly enhanced if it had been more adequately illustrated. In the whole book there is but one plate containing 14 line drawings. Except for this defect it is an excellent piece of work.

REPORT OF THE HARVARD BOTANICAL GARDENS, SOLEDAD ESTATE, CIENFUEGOS, CUBA. (*Atkins Foundation.*) *1900—1926.*
By Robert M. Grey.
Harvard University Press
\$1.25 *Cambridge, Mass.*
$7\frac{5}{8}$ x $10\frac{5}{8}$; 113 (paper)

A report, covering a quarter of a century, of the Harvard Botanical Gardens at Cienfuegos. It is chiefly concerned with meteorological and phenological data, and a description of introduced and acclimatized forms.

MORPHOLOGY

ANATOMIE COMPARÉE DU CERVEAU.
By R. Anthony. *Gaston Doin et Cie*
70 francs $6\frac{1}{8}$ x $9\frac{3}{8}$; 359 (paper) *Paris*

A comparative morphological treatise, having for its aim a better understanding of the human brain. The first chapter embodies a detailed and interesting discussion of brain-weights and their significance. There then follow morphological

discussions of the telencephalon, the rhinencephalon, the neopallium, and the grey nuclei of the telencephalon. There are 234 illustrations, and an author, but no subject index. The book will form a useful addition to anatomical libraries.

ENTWICKLUNGSGESCHICHTE DES MENSCHEN *mit Berücksichtigung der Wirbeltiere.*
By L. Michaelis. *Georg Thieme*
8.70 marks *Leipzig*
5 x 7¾; viii + 253 + 4 plates

This is the tenth edition, revised and enlarged by Prof. Richard Weissenberg, of an elementary textbook of human embryology. It follows conventional lines but is brought thoroughly up to date.

PHYSIOLOGY

THE ENDOCRINES IN GENERAL MEDICINE.
By W. Langdon Brown.
Paul B. Hoeber, Inc.
$3.00 5⅝ x 8½; vii + 144 *New York*

This volume is primarily intended for the general practitioner. Based largely on the author's personal laboratory and bedside experience, the book first introduces the reader to the "biological position of the endocrine system in relation to the visceral nervous system, which seems to me to provide a key to its mode of action." Throughout the book the discussions of the physiology of the various endocrine glands are freely illustrated by the citation of clinical cases. While the chapters are necessarily brief, there is not so much condensation as to make difficult reading. The book is well indexed, but lacks any bibliography, which would seem to indicate that the author presupposes a lack of time or possibly interest on the part of his audience to follow up the subject in more technical literature. Dr. Brown sees the future of endocrinology as follows:

> As the psychological make-up depends in large part on the endocrine pattern, endocrinology will play an increasing part in the study of psychoneuroses, and in the rational determination of vocation; pharmacology will come to the aid of substitution therapy; greater use will be made of the antagonisms and coöperations between the different endocrines; and endocrinology will help in the treatment of hepatic diseases.

THE COMPARATIVE PHYSIOLOGY OF INTERNAL SECRETIONS.
By Lancelot T. Hogben.
The Macmillan Co.
$4.00 5½ x 8¼; 148 *New York*

This is a concise but critical and thorough review of the present state of knowledge regarding the physiology of the endocrine glands. The material is discussed under the following heads: Chemical co-ordination; adrenaline and neuromuscular co-ordination; internal secretion and the chromatic function; endocrine factors in secretory processes; the relation of internal secretions to vasomotor regulation; endocrine factors in metabolism; the rôle of the ductless glands in developmental processes.

The book will be of great value for reference purposes in the field of endocrinology. This being so it seems a pity that the documentation of the literature is not more comprehensive. At the end of each subject section a short list of the more important references is given, but the exact location of many of the citations in the text is difficult or impossible to find anywhere in the book. This is a matter of no great moment to the specialist in the field, who already knows the literature, but diminishes the otherwise great use-

fulness of the book to the beginning student of endocrinology.

THE GLANDS OF DESTINY. (*A Study of the Personality.*)
By Ivo Geikie Cobb. *The Macmillan Co.*
\$3.00 $4\frac{3}{4} \times 7\frac{1}{4}$; vii + 295 *New York*

This is a readable discussion of the effects produced by the glands of internal secretion on the mind and character of the individual. It is one of a number that have appeared recently, all of them designed for lay consumption. Although the author shows a commendable tendency to stick to facts the spirit of the journalist occasionally gets the better of him as on pages 82 and 83 where we learn that, "It is apparent that the individual capable of a speedy response is, in all probability, one who has an active adrenal medulla," and that "The adrenal type is a quiet, alert and successful one." To be sure his conscience bothers him a bit, and to show that he might be worse he quotes Berman to the effect that one "adrenal-centered type" is "Hairy, dark, masculinity marked, with tendency to diphtheria and hernia."

ALLGEMEINE PHYSIOLOGIE. *Handbuch der normalen und pathologischen Physiologie. Band I.*
64 marks (paper) *Julius Springer*
69.60 marks (bound) *Berlin*
$6\frac{3}{4} \times 10\frac{1}{4}$; xii + 748

This first volume of a new, comprehensive Handbook of physiology, which is to be completed in some 17 volumes, under the general editorship of Professors Bethe, von Bergmann, Embden, and the late Prof. Ellinger, contains the following articles: Definition of life and the organism, by J. v. Uexküll; the chemical system of the organism and its energy relation, by W. Lipschitz; enzymes, by P. Rona; physical chemistry of colloid systems, by G. Ettisch; bioenergetics, by H. Zwaardemaker; irritability and stimulation, by P. Broemser; general conditions of life, by A. Pütter; interchange of material between the protoplast and its surroundings, by R. Höber; ion effects, by H. Reichel and K. Spiro; narcosis, by H. H. Meyer; protoplasmic poisons, by H. Reichel and K. Spiro; the functional significance of cell structure, particularly with reference to the nucleus, by G. Hertwig; division of labor in higher organisms, by O. Steche; parasitism and symbiosis, by O. Steche; evolution and adaptation, by J. v. Uexküll; the circulation of matter in nature, by K. Boresch. There is a subject, but no author index. The book will be a useful reference source for the general biologist.

ELEMENTS OF PHYSIOLOGY. *For Students of Medicine and Advanced Biology.*
By Ernest G. Martin and Frank W. Weymouth. *Lea and Febiger*
\$8.00 net $5\frac{3}{4} \times 9\frac{1}{4}$; 784 *Philadelphia*

The guiding ideas around which this new textbook of physiology is written are first that living protoplasm is a system of molecules and ions, hence understanding of its structure and functioning is to be sought by attempting to apply to it the physical, physico-chemical and chemical laws by which the interrelations of molecules and ions are described. The second basic idea is that every protoplasmic cell is inherently a self-sustaining system. Consequently, if it is continuously provided with a proper environment, it should continue to live and function indefinitely (subject, of course, to the possible influence of intrinsic senility).

The material is organized under the following general heads: The nature and capacities of protoplasm; cell environment; bodily maintenance; external adjustment. The book is well written, and will be found useful by all teachers of physiology.

HIPPOCRATES. *Vol. III.*
Translated by E. T. Withington.
William Heinemann Ltd.
Cloth 10s. net *London*
Leather 12s. 6d. net
$4\frac{3}{8} \times 6\frac{3}{4}$; xxvii + 455

This recent addition to the Loeb Classical Library deals with the surgical works of Hippocrates, which are in some respects the most important of his writings. The editor and translator is a private English scholar, not connected with any university, whose thorough knowledge of Greek scientific and medical writings has been utilized in the preparation of the new Liddell and Scott lexicon.

This volume will interest all biologists, as well as medical men, who are interested in the historical side of their subject. The chief thing which strikes the reader is, once more, the extraordinary modernity of the ancient Greeks.

THE HARVEY LECTURES. *1926–1927. Series XXII.*
The Williams & Wilkins Co.
\$4.00 $5\frac{1}{4} \times 8$; 164 *Baltimore*

The lectures included in this volume have the following titles: Origin and dissemination of tuberculosis according to recent investigations, by Fred Neufeld; the nature of the living cell as revealed by microdissection, by Robert Chambers; some problems concerning the gastric juice, by Leonor Michaelis; analysis of the action potential in nerve, by Joseph Erlanger; health and activity, by Edgar L. Collis; organic chemistry—its relation to medicine, by Richard Willstätter; the exchange of material between the erythrocyte and its surroundings, by Merkel H. Jacobs.

The lectures of Dr. Chambers, Dr. Willstätter, and Dr. Jacobs are of particular interest to the general biologist. Unfortunately there is no index.

QUESTIONS PHYSIOLOGIQUES D'ACTUALITÉ.
By Léon Binet. *Masson et Cie*
18 francs $6\frac{1}{4} \times 9$; 227 (paper) *Paris*

This volume contains a series of lectures and critical reviews covering a wide range of particularly lively physiological subjects. The material was presented as lectures, in what must have been an unusually interesting course inaugurated by the author, under the Faculty of Medicine at Paris, in the academic year 1925–1926. Some of the subjects discussed are: Histophysiological studies of the lung; relations between the intestine and the lung; physiological observations on mountain sickness; anticoagulants; experimental study of haemorrhage; thirst; the physiology of sleep; internal factors of growth; physiological study of tobacco smoking; etc.

THE MECHANICS OF THE DIGESTIVE TRACT. *An Introduction to Gastroenterology.*
By Walter C. Alvarez. *Paul B. Hoeber, Inc.*
\$7.50 net 6×9; xix + 447 *New York*

The second edition of a well-known and valuable treatise on the physiology and pathology of the alimentary canal. The revision and addition of material has been

so great as to make this edition practically a new book, and a reliable and authoritative digest of what is known in this branch of physiology. The book is abundantly illustrated and contains a bibliography of 900 titles. Dr. Alvarez says that this bibliography "is probably the best part of the book." With this we cannot agree. The scientific and literary skill with which this mass of raw material has been analyzed and integrated by Dr. Alvarez is a contribution of first rate importance.

LIVING MACHINERY.
By A. V. Hill. *Harcourt, Brace and Co.*
$3.50 $5\frac{1}{2} \times 8\frac{1}{4}$; xxi + 306 *New York*

This volume of Lowell lectures, by the distinguished Nobel laureate in physiology, is an extremely interesting, well-written, popular exposition of the present status of knowledge of nerve-muscle physiology. At least the first six lectures are such, being essentially a repetition of the author's Christmas lectures at the Royal Institution in London. The last two are more philosophical in character and deal respectively with the position of physiology among the sciences, and a critical discussion of mechanism and teleology. The whole makes excellent reading for everyone, biologist or layman.

NUTRITION AND DIET IN HEALTH AND DISEASE.
By James S. McLester.
W. B. Saunders Co.
$8.00 $6 \times 9\frac{1}{4}$; 783 *Philadelphia*

This treatise on nutrition is written particularly for the medical man. Nearly two-thirds of the book is devoted to the discussion of nutrition in disease. A great deal of attention is given to dietaries supposed to be particularly suited to various diseased conditions. The interest of the book is therefore rather special than general, but it accomplishes very well the task set. Practising physicians will find it useful as a comprehensive reference work.

THERMIONIC PHENOMENA.
By Eugène Bloch. Translated by J. R. Clarke. *E. P. Dutton and Co.*
$2.50 $4\frac{3}{4} \times 7\frac{1}{4}$; x + 145 *New York*

This volume will be of particular interest only to the worker in the field of biophysics. Bringing together the important advances made in knowledge concerning emissions from heated bodies the author shows where confusion in this subject still exists and where there is need for the concentrated attack of investigators. A short chapter giving an account of some of the applications of thermionic phenomena, and author and subject indices add to the value of the treatise.

PRINCIPES DE PHARMACODYNAMIE.
Constitutions Chimiques; Propriétés Physiologiques.
By L. Hugounenq and G. Florence.
Masson et Cie
40 francs *Paris*
$6\frac{1}{4} \times 9$; viii + 391 (paper)

A systematic treatise on pharmacology approached from the point of view of correlating chemical structure and physiological effect. The book opens with an excellent historical account of research in this field. It is extensively and internationally documented.

BIOCHEMISTRY

PHYSICAL CHEMISTRY AND BIOPHYSICS.
By Matthew Steel.
John Wiley and Sons, Inc.
$4.00 5¾ x 9; x + 372 *New York*

A textbook in which the rudiments of physical chemistry are treated in a manner especially adapted to the requirements of medical and biological students. It is so arranged as to make it suitable for a course continuing through at least a third of an academic year. The illustrations of the application of physico-chemical principles are taken from the fields of biology, physiology and medicine. Considerable attention is given to the nature and structure of matter, while in the chapter on the Colloidal State of Matter the work of Jacques Loeb on proteins is treated with considerable detail. A number of illustrations and a complete author and subject index increase the usefulness of the book.

ÜBER DIE KATALYTISCHEN WIRKUNGEN DER LEBENDIGEN SUBSTANZ. *Arbeiten aus dem Kaiser Wilhelm-Institut für Biologie, Berlin-Dahlem.*
Edited by Otto Warburg. *Julius Springer*
36 marks (paper) *Berlin*
37.80 marks (bound)
6¾ x 9¾; vi + 528

A collection of papers by Warburg and his students, arranged under three general heads: Respiration and fermentation; carbonic acid and nitrate assimilation; and the catalytic action of growing cells. There is appended a bibliography covering four pages, but unfortunately there is no index, which diminishes the usefulness of a compilation of separate studies like this. It is, however, a real service to have available in one volume all these scattered papers giving the results of the very important work that Dr. Warburg is doing on cellular metabolism and the cancer problem.

DIE BESTIMMUNG DER WASSERSTOFFIONENKONZENTRATION VON FLÜSSIGKEITEN. *Ein Lehrbuch der Theorie und Praxis der Wasserstoffzahlmessungen in elementarer Darstellung für Chemiker, Biologen und Mediziner.*
Dr. Ernst Mislowitzer. *Julius Springer*
Paper: 24 marks *Berlin*
Bound: 25.50 marks
6¾ x 9½; x + 378

The introduction by Professor Rona states that this book was prepared at his suggestion to fill a gap in the German literature occasioned by the fact that the first edition of Michaelis' treatise on hydrogen ion concentration, "ein Meisterwerk didaktischer Kunst," has for many years been out of print. The scope of the present work is sufficiently indicated in its title. There is a bibliography covering some 32 pages.

DIE METHODIK DER FERMENTE. *Lieferung I.*
Edited by Carl Oppenheimer and Ludwig Pincussen. *Georg Thieme*
28 marks *Leipzig*
7⅝ x 10⅝; x + 320 (paper)

This is the first part of what is to be a large collective reference work on enzymes. It contains 20 chapters, of varying lengths, contributed by a number of different authorities in this field. The volume is divided into two parts, of which the first deals with the general methodology of enzyme investigations, physical, physico-chemical, and chemical. The

second part deals with the substrates upon which enzymes act. The whole treatise, when completed, promises to be an extremely useful reference work for biologists.

INVESTIGATIONS ON CHLOROPHYLL. *Methods and Results.*
By Richard Willstätter and Arthur Stoll. Authorized English Translation from the German by Frank M. Schertz and Albert R. Merz. *Frank Schertz*
1305 Farragut St., N.W., Washington, D.C.
$4.50 6 x 9; xii + 385 + 11 plates

The translators have performed a real public service to American and English biologists in publishing this English translation of the fundamental researches of Willstätter and Stoll on chlorophyll. Since they have published the book at their own expense and risk it is to be hoped that American biologists will indicate their appreciation by buying it for their laboratories and libraries. The translation is very well done.

L'URÉE (*Recherches de chimie analytique, biologique et agricole*). LES FONCTIONS. *Dinaphtopyranol, Xanthydrol et Sel de Pyryle (Chimie organique).*
By Richard Fosse.
Les Presses Universitaires de France
50 francs 6 x 9½; xii + 303 *Paris*

This is one of a series of monographs on biologic problems. Fosse is the discoverer of the xanthydrol reaction for urea. In this volume he summarizes his studies on ureogenesis and the distribution of urea in various animals and plants. As he rarely touches on the work of others, this volume can hardly be compared with the monographs of Werner and Fearom.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *II. Band. V. Lieferung.*
By Otto Fürth. *F. C. W. Vogel*
15 marks *Leipzig*
7 x 10; v + 185 (paper)

Another section of the Fürth textbook, earlier parts of which have been noticed in these columns. The present section deals with the metabolism of purins and carbohydrates generally, including at the end a chapter on lactic acid, as the most important intermediate product in the breaking down of sugar.

KURZES LEHRBUCH DER PHYSIOLOGISCHEN CHEMIE.
By Paul Hári. *Julius Springer*
18 marks (paper) *Berlin*
19.50 marks (bound)
6⅞ x 8¾; xii + 407

The third editon of a standard text. Considerable additions have been made to bring the book up to date, and the material has been rearranged somewhat for pedagogical reasons.

SEX

SEXUAL APATHY AND COLDNESS IN WOMEN.
By Walter M. Gallichan.
T. Werner Laurie, Ltd.
7s. 6d. 4⅞ x 7⅜; 183 *London*

Another volume for the benefit of the sexually unsatisfied. In our attempt to bolster up our present civilized mode of living has it not been overlooked that through countless ages past there is no evidence that man had any more sex problems than a guineapig has? Substantially down until the Puritans saddled the west-

ern world with their dour philosophy the only books about *It* were humorous ones. This is a sound attitude, as Dr. Clendening has lately emphasized. So far as may be judged from historical and general literature, sexual apathy and coldness is a modern phenomenon. Mr. Gallichan says the usual things about its being due to inadequate education of girls in sex matters, to lack of understanding on the part of men, to the complexity of modern life, etc. We have looked in vain for anything in the way of an original note in the book.

BESTIMMUNG, VERERBUNG UND VERTEILUNG DES GESCHLECHTES BEI DEN HÖHEREN PFLANZEN. *Handbuch der Vererbungswissenschaft. Band II. Lieferung 3 (II, C.).*
By C. Correns. *Gebrüder Borntraeger*
19.20 marks *Berlin*
7 x 10¾; iii + 138 (paper)

This section of the Baur-Hartmann handbook of genetics deals with the problem of sex in plants, by the foremost living authority in this field. It maintains the high standard set by the other parts of this great undertaking which have so far appeared. There is a bibliography covering nine pages.

CONTRACEPTION (*Birth Control*). *Its Theory, History and Practice (second edition).*
By Marie Carmichael Stopes.
John Bale, Sons and Danielsson, Ltd.
25 shillings *London*
5½ x 8½; xxvi + 480

This new edition of Dr. Marie Stopes' *vade-mecum* for newlyweds still embodies all the author's well-known enthusiasm for more and better sex life in the home. In fact the book is not basically altered from the first issue. About 60 pages of new material have been added, but the growth between the first and second editions has been intersusceptive. The book cannot legally be imported into this land, quaintly said to be "of the free." Reginald, the Office Boy, says he found our copy on the doorstep one morning.

PSYCHOLOGY AND BEHAVIOR

SPEECH. *Its Function and Development.*
By Grace Andrus de Laguna.
Yale University Press
$5.00 *New Haven, Conn.*
5½ x 8¼; xii + 363

A thorough-going attempt at a reasonable solution of an extremely difficult and complex problem, the origin of speech. The first part of the book is devoted to the development of the thesis that speech began when man's ancestors came down from the trees and began to hunt on the ground. Its origin was in the animal cry "in order to meet the demands of expanding group life."

> The evolution of language, marked by the differentiation of the proclamation, which prepares but does not precipitate response, and of the supplementary command, with its power to initiate and control particular acts, is an essential condition for the complex and varied coöperation that is involved in human hunting.

The second part of the book attempts to trace the evolution of thought which paralleled that of speech. A theory of the origin and development of the naming of objects is developed. The third part of the book recapitulates the preceding arguments from the objective point of view.

The book is a valuable contribution to the literature of human biology.

AN EXPERIMENT WITH TIME.
By J. W. Dunne. *The Macmillan Co.*
$2.50 $5\frac{1}{2} \times 8\frac{3}{8}$; 208 *New York*

This is an interesting, if not entirely convincing, attempt to show that man's mind is capable of the correct anticipation of future events in the phenomenal world, as a definite and regular thing in contrast to a merely accidental coincidence. The book starts with an account of the author's dreams, and ends with a new theory of the universe. It thus traverses a good deal of ground. The pathway gets very obscure at times, and we fancy that most readers will have a good deal of difficulty in following Mr. Dunne all the way. But the facts which he records are extraordinary, and cannot be accounted for by any other theory at the moment. So on this account, if no other, Mr. Dunne's theory deserves respectful consideration.

STAMMERING. *A Psychoanalytic Interpretation.*
By Isador H. Coriat.
Nervous and Mental Disease Publishing Co.
$2.00 6 x 9; viii + 68 *New York*

The author is of the opinion that "stammering is one of the severest forms of the psychoneuroses and is not merely a tic, an obsession, an auditory amnesia, a spasm of coördination of the muscles involved in speech, neither is it produced by a conflict of languages, according to the usual superficial interpretations of its pathogenesis. It is preëminently what may be termed an 'oral neurosis.' "

This thesis is supported by psychoanalytic arguments.

Excessive mouth erotism is, therefore, the basis of stammering, a projection from the unconscious of the precipitated components of the oral stage of libido development. The mouth has become the principal and all-powerful organ of libidinal pleasure, which is gratified, although against resistance, by the oral discharge of speech. In several instances there was noted, in addition to the frequent sucking movements with the lips and excessive salivation during the paroxysm of stammering, deep breathing, rapid heart beat, perspiration, yawning; this was followed by a feeling of relaxation after enunciation of a difficult word. Here there could be observed an actual reproduction, in adult life, of the relationship of the infant to the nipple, a gratification of the oral-erotic zone in pleasure sucking reënacted in maturity. The original attachment of the sexual excitation to the nutritional instinct, that is, the oral phase of the libido, still dominates the adult stammerer, in fact, the persistence of this phase into maturity, produces stammering in order to satisfy a compulsive-repetition, which resembles a tic.

A stutterer will never seem the same to us after this!

A STUDY OF NATIO-RACIAL MENTAL DIFFERENCES. *Genetic Psychology Monographs Vol. 1, Nos. 3 and 4.*
By Nathaniel D. Mttron Hirsch.
Clark University
$3.00 (paper) *Worcester, Mass.*
$3.50 (cloth) $5\frac{3}{4} \times 9$; 168

In this monograph the author gives a report of his study on the mental capacity of some of the nationalities to be found in the American population. The subjects were school children, American born, both of whose parents were foreign born and of the same nationality. Two other groups were included in the study—white American children and a group of Afro-American children. The author first gives a brief summary of some of the results and conclusions of other studies upon racial and national psychological differences; then follow chapters in which the tests given the children are described in detail, and the results analyzed. The highest testing children were Polish Jews. The last three

chapters are devoted to an hypothesis which is deemed a fair and proper interpretation of the data collected.

The author believes that intelligent action can lead to the blending of certain sub-races in the American population which would result in a desirable variability in the new stock and that such blending would produce many great men and geniuses. "An American art, drama, music and especially a new religion would arise as the creations of the genius of the new Natio-Race."

MY HAPPY CHIMPANZEE. *The Adventures of Mary, the Wonderful Chimpanzee, at the Seaside.*
By Cherry Kearton. *J. W. Arrowsmith, Ltd.*
5 shillings 5½ x 7½; 124 *London*

This little book, while perhaps not quite so appealing to the lover of animals as the author's earlier book, "My Friend Toto," consists of another series of interesting and amusing anecdotes about the very human behavior of an almost human creature.

DE L'EXPLICATION DANS LES SCIENCES.
By Émile Meyerson. *Payot*
60 francs 5½ x 9; 784 (paper) *Paris*

A philosophical treatise on the theory of knowledge of first rate significance to all scientific men, and especially biologists. Apart from the stimulating qualities of the author's own particular brand of monism, the work is valuable as a history of scientific ideas and methodology.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

PROPHYLAXIE ANTIVÉNÉRIENNE INDIVIDUELLE À TRAVERS LES AGES. *Essai historique.*
By E. L. A. Baude.
Librairie E. le François
6 francs 6¼ x 9¾; 47 (paper) *Paris*

This is an entertaining historical account of one aspect of man's struggle with a difficult general problem, namely, how to have one's cake and eat it too. Anaxitoteles made the sage remark that the worship of no goddess is pleasanter than that of Venus. But the consequences are all too often depressing, not to say disastrous. Dr. Baude says that personal prophylaxis against venereal disease was first put on a really scientific basis by Metchnikoff in 1906. Before that time the matter had been either in the hands of quacks or of honest but stupid physicians who thought they were getting results but weren't.

This scholarly treatise of Dr. Baude's, with its bibliography of 79 titles, will form the material for a learned footnote in that *magnum opus*, in elephant folio, *The Natural History of Copulation*, to the preparation of which certain distinguished biologists propose to devote the declining years of their lives.

A BOOK OF FOOD.
By P. Morton Shand.
Alfred A. Knopf, Inc.
$4.00 5½ x 8; 319 *New York*

Although not a cook book this volume is about food in the home. In the preface the author says that his remarks "are addressed not merely to gourmets, to all curious and adventurous spirits in the domain of gastrosophy, but also to

malcontents with the food we eat in England today; and to men, rather than to women, among my long-suffering compatriots."

One might venture to suggest that this volume be read shortly before meal time. Not that the book is only readable under such conditions. Far from it! But, like an *Amer Picon*, a slightly famished state will whet the reader's perceptions, and along with the author his enthusiasms for *oeufs-au-plat* and *Sole à la Meunière* will carry him to happy realms. American women, whose customary source of food lore is that of the monthly magazine or daily paper, should find this book a welcome diversion.

THE IMPORTANCE OF BEING HISTORICALLY MINDED.
By Wm. Allen Pusey.

American Medical Assoc. Press
$4\frac{1}{2} \times 6\frac{3}{4}$; 22 *Chicago*

An amusing and at the same time penetrating little tract on the present status of medicine, philosophically considered. The author is a wise old clinician, and in this address gives the brash young laboratory boys, whose behavior indicates that they suppose scientific medicine began about a fortnight after they got started, a good deal to think about. It is an excellent piece of debunkification, a word that the office cat brought in the other day.